SHOUT
SHARE
IT

HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

LIBRARY
AUG 1 5 1991
HARVARD
UNIVERSITY

THE
GREAT BASIN
NATURALIST

50-YEAR INDEX

VOLUMES 1–50, 1939–1990

VOLUME 51 № 1 — MARCH 1991

BRIGHAM YOUNG UNIVERSITY

GREAT BASIN NATURALIST

Editor

James R. Barnes

290 MLBM
Brigham Young University
Provo, Utah 84602

Associate Editors

Michael A Bowers
Blandy Experimental Farm
University of Virginia
Box 175
Boyce, Virginia 22620

Jeanne C. Chambers
USDA Forest Service Research
860 North 12th East
Logan, Utah 84322-8000

Jeffrey R. Johansen
Department of Biology
John Carroll University
Cleveland, Ohio 44118

Paul C. Marsh
Center for Environmental Studies
Arizona State University
Tempe, Arizona 85287

Brian A. Maurer
Department of Zoology
Brigham Young University
Provo, Utah 84602

Jimmie R. Parrish
Department of Zoology
Brigham Young University
Provo, Utah 84602

Editorial Board. Richard W. Baumann, Chairman, Zoology; H. Duane Smith, Zoology; Clayton M. White, Zoology; Jerran T. Flinders, Botany and Range Science; William Hess, Botany and Range Science. All are at Brigham Young University. Ex Officio Editorial Board members include Clayton S. Huber, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications; James R. Barnes, Editor, *Great Basin Naturalist*.

The *Great Basin Naturalist*, founded in 1939, is published quarterly by Brigham Young University. Unpublished manuscripts that further our biological understanding of the Great Basin and surrounding areas in western North America are accepted for publication.

Subscriptions. Annual subscriptions to the *Great Basin Naturalist* for 1991 are $25 for individual subscribers, $15 for student and emeritus subscriptions, and $40 for institutions (outside the United States, $30, $20, and $45, respectively). The price of single issues is $12. All back issues are in print and available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to the Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, UT 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining the *Great Basin Naturalist* through a continuing exchange of scholarly publications should contact the Exchange Librarian, Harold B. Lee Library, Brigham Young University, Provo, UT 84602.

EDITORIAL PRODUCTION STAFF

JoAnne Abel	Technical Editor
Carolyn Backman	Assistant to the Editor
Heidi Larsen	Production Assistant

Copyright © 1991
by Brigham Young University

ISSN 0017-3614
7-91 1500 52075

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 51 | 31 MARCH 1991 | NO. 1

Great Basin Naturalist 51(1), 1991, pp. 1–108

The Great Basin Naturalist
50-YEAR INDEX
Volumes 1–50, 1939–1990

Jody N. Reid[1], Richard D. Jensen[1], and Nathan M. Smith[2]

PREFACE

For the past 50 years, the *Great Basin Naturalist* has published results of natural history studies in the intermountain region. Vasco M. Tanner, a protégé of David Starr Jordan, deserves recognition for establishing the journal, maintaining it, and securing its good reputation for the first 30 years. (More information concerning Dr. Tanner and his contributions can be found in Vol. 30, No. 4.) The *Great Basin Naturalist's* second editor, Stephen L. Wood, continued to promote its growth and recognition for the next 20 years. Since September 1989 James R. Barnes has been the editor. Very few regional natural history journals can claim the distinction of having survived for half a century and having had only two editors during that time.

Today the *Great Basin Naturalist* is firmly established as a forum for reporting research; its contents exhibit a range of emphasis in natural history topics and methods. In the earlier years papers centered on descriptive research, while later papers have more often been analytical. Both early and more recent studies continue to be utilized, providing invaluable groundwork for further synthesis and new conclusions.

Volume indices, printed at the end of each year, have facilitated finding what has been published in the journal. A 30-year index was compiled by Vasco M. Tanner when he retired as the first editor. Basically an author-title index with a comprehensive listing of new taxa, it was very helpful in locating information from that time period. Since then only volume indices have been published. Before Stephen L. Wood retired, he felt it would be valuable to compile a 50-year index to the *Great Basin Naturalist*. The authors of this index approached Dr. Wood and offered to do the work on the project. As life science librarians, we recognized the benefits such an index could provide.

Our intent in creating this index is to enable researchers to readily locate articles of interest, descriptions of new species, and other

---

[1] Science Library, Harold B. Lee Library, Brigham Young University, Provo, Utah 84602.
[2] School of Library and Information Sciences, Brigham Young University, Provo, Utah 84602.

information contained in the past 50 volumes of the *Great Basin Naturalist*.

INTRODUCTION

This index consists of two parts. The first is an author-title index. Entries are alphabetical (last name first) by senior author with cross references from secondary authors to the senior author. Under an author's name, articles written solely by the author are listed first; articles with one co-author come next and are followed by articles with two or more co-authors. Co-authors are listed in the order they appear on the title page of the article. Example:

Cottam, Clarence, Cecil S. Williams, and Clarence A. Sooter. Some unusual winter visitors or late migrants to the Bear River marshes, Utah. 3:51–53.

Sooter, Clarence A. *See* Cottam, Clarence 3:51–53.

Williams, Cecil S. *See* Cottam, Clarence 3:51–53.

The second part is a subject index. Most articles received three or four subject entries. These terms were taken from the title and abstract and were sorted so that each significant term became a main heading. The other subject terms used for each article are listed as subheadings under the main headings to help locate specific articles. Following each entry are the *Great Basin Naturalist* volume and page numbers where the article can be found.

In indexing names of plants and animals we used the following guidelines:

(1) If both Latin and English names appeared in the title or abstract, both were used in the index, except in most taxonomic articles. In taxonomic articles the Latin names took precedence.

(2) If only Latin names were present in the title or abstract, then only Latin names were used in indexing.

(3) If only English (common) names were in the title or abstract, then only those were used in the index.

When indexing taxonomic articles, we primarily used only Latin names. Articles were indexed according to the lowest taxonomic group that included all taxa discussed. Additional entries were made for all new genera, species, subspecies, or varieties. Also, entries were generally made for class in vertebrates, order in invertebrates, and family in plants. The new portion of the name was then set in boldface type in lieu of other designations such as n.sp. Example (brackets [ ] indicate intervening entries):

Acari
  Ametroproctus, systematics, United States 28:44–46
  [ ]
  Oppia coloradensis, systematics, Colorado 29:133–136

Ametroproctus oresbios 28:44–46

Oppia coloradensis 29:133–136

New combinations were not indexed due to space limitations. New records received one entry per article unless only two names were listed. When only two new records were given, they each received a separate entry. All new records can be found under the heading "New records," followed by the name (usually in Latin) and then locality. Checklists were designated by subheadings under the group name and/or location of the checklist. Keys were indexed in this same way. Example:

New records
  [ ]
  Hindia sphaeroidalis, Nevada 36:206–210

Plants
  [ ]
  Vascular
    [ ]
    Bighorn Canyon, Wyoming-Montana, checklist 45:734–746

Polygonaceae
  [ ]
  Eriogonum pauciflorum
    Systematics, keys 27:102–117

Geographic names were used as main headings whenever they were significant to the article. State or region was followed by the locality within that area. Example:

Nevada
  [ ]
  Pyramid Lake
    [ ]
    Sacramento perch, life history 41:278–289

An additional main entry was made for the locality name followed by the state or region. When a geographic name was used as a subheading, the locality was always listed first, followed by the state or region. Example:

Pyramid Lake, Nevada
  [ ]
  Sacramento perch, life history 41:278–289

Subject headings beginning with arabic numbers (i.e., 2,4-D) are listed after the Z's at the end of the alphabetic terms.

Many multiple-term main headings were inverted to place related topics in closer proximity. This applies primarily to English names of organisms, general subjects, and geologic time periods. Example:

Grouse
  Blue
    Effects of summer weather on harvest 42:91–95
    Feeding habits 46:123–127
    Hatching chronology 46:745–748
  Sage
    Big sagebrush, selection 48:274–279
    Habitat use by breeding males 49:404–407

No attempts were made to control vocabulary and nomenclature in creating the index. The terminology employed by authors in titles and abstracts was used in the index, except in systematic articles where we used the term systematics to include taxonomy, descriptions, etc.

We hope the index will be accurate, easy to use, and helpful in finding the valuable information published in the first 50 volumes of the *Great Basin Naturalist*.

ACKNOWLEDGMENTS

Special acknowledgments are due the Harold B. Lee Library administration and the School of Library and Information Sciences for providing the time and facilities for preparation of this index. Student research assistants Jessica Draper, Charles Kalua'u, Elizabeth Slaughter, Anna Wu, and Zhang Limin spent many hours proofreading and making corrections. Erva Rieske and her students in the library secretarial pool entered data for the author/title index. Kal Larsen, of library computer operations, provided invaluable computer programming. The authors express their appreciation to each of these people who made an arduous task easier.

PART I

AUTHOR-TITLE INDEX

(To determine the year of publication, add 1940 to volume numbers beginning with volume 10. During World War II publication of the *Great Basin Naturalist* was, of necessity, less structured. Consequently, some early volumes cover more than a year; others are limited to one issue consisting of the four quarterly numbers. Consult a library for accurate publication dates for volumes 1-9.)

A

Adkins, Betty S. *See* Elliott-Fisk, Deborah L. 43:377-384.

Albee, Beverly. *See* Welsh, S. L. 41:1-108.

Aldon, Earl F. Long-term plant survival and density data from reclaimed southwestern coal mine spoils. 41:271-273.

______. Vegetation parameters for judging the quality of reclamation on coal mine spoils in the Southwest. 44:441-446.

Alexander, Charles P. A new net-winged midge from Idaho (Blepharoceridae, Diptera). 25:1-3.

______. New or little-known Tipulidae from Middle America (Diptera). I. 30:232-241.

______. Undescribed species of Nearctic Tipulidae (Diptera). I. 21:79-86.

______. Undescribed species of Nearctic Tipulidae (Diptera). II. 22:1-7.

______. Undescribed species of Nearctic Tipulidae (Diptera). III. 23:159-165.

______. Undescribed species of Nearctic Tipulidae (Diptera), IV. 24:19-25.

______. Undescribed species of Nearctic Tipulidae (Diptera). V. 24:117-122.

______. Undescribed species of Nearctic Tipulidae (Diptera), No. VI. 25:49-53.

______. Undescribed species of Nearctic Tipulidae (Diptera), No. VII. 26:1-8.

______. Undescribed species of Nearctic Tipulidae (Diptera), VIII. 28:16-23.

______. Undescribed species of Nearctic Tipulidae (Diptera), IX. 28:113-123.

______. Undescribed species of Nearctic Tipulidae (Diptera), X. 29:1-10.

______. Undescribed species of Nearctic Tipulidae (Diptera), XI. 33:189-196.

______. Undescribed species of western Nearctic Tipulidae (Diptera). I. 4:89-100.

______. Undescribed species of western Nearctic Tipulidae (Diptera). II. 5:93-103.

______. Undescribed species of western Nearctic Tipulidae (Diptera). III. 18:31-36.

______. Undescribed species of western Nearctic Tipulidae (Diptera), IV. 21:10-16.

Alldredge, A. William. *See* Halford, Douglas K. 47:105-109.

Alldredge, J. Richard. *See* Knick, Steven T. 44:70-74.

Allen, Douglas W. *See* Cox, George W. 47:609-619.

Allen, Richard K. and Chad M. Murvosh. Leptophlebiidae of the southwestern United States and northwestern Mexico (Insecta: Ephemeroptera). 47:283-286.

Allred, Darin B. *See* Jorgensen, Clive D. 46:173-174.

Allred, Dorald M. Additional records of mutillid wasps from the Nevada Test Site. 33:156-162.

______. Ants of Utah. 42:415-511.

______. Arachnids as ecological indicators. 35:405-406.

______. Bees of the Nevada Test Site. 29:20-24.

______. Bite of wolf spider. 38:478.

______. A *Chiracanthium* spider bite. 40:116.

______. Ecological notes on recently described myriapods from Nevada. 31:161-163.

______. Fleas of the National Reactor Testing Station. 28:73-87.

______. Lepidoptera of the Nevada Test Site. 29:42.

______. Mammalian ectoparasite consortium at the National Reactor Testing Station. 31:77-82.

______. Mites found on mice of the genus *Peromyscus* in Utah. I. General infestation. 16:23-31.

______. Mites found on mice of the genus *Peromyscus* in Utah. V. Trombiculidae and miscellaneous families. 17:95-102.

______. Mites on grasshopper mice at the Nevada atomic test site. 22:101-104.

______. Note of phalangids at the Nevada Test Site. 25:37-38.

______. Notes on Nevada solpugids. 32:120.

______. Plague important fleas and mammals in Utah and the western United States. 12:67-75.

______. Records of Coreidae (Hemiptera) from the Nevada Test Site. 33:123.

______. Scorpions of the National Reactor Testing

Station, Idaho. 33:251-254.
______. Small mammals of the National Reactor Testing Station, Idaho. 33:246-250.
______. Spiders of the National Reactor Testing Station. 29:105-108.
______. Swarming of the western harvester ant, *Pogonomyrmex occidentalis*. 40:165-166.
______. An unusual population of spiders in Utah. 33:51-52.
______. Unusual records of Utah mites. 26:34.
______. An unusual spider bite. 34:82.
______ and D Elden Beck. A list of Scarabaeidae beetles of the Nevada Test Site. 25:77-79.
______ and D Elden Beck. A new species of *Acomatacarus* (Acarina, Trombiculidae) from Utah. 13:87-90.
______ and D Elden Beck. Spiders of the Nevada Test Site. 27:11-25.
______ and Arthur C. Cole. Ants from northern Arizona and southern Utah. 39:97-102.
______ and Arthur C. Cole. Ants of the National Reactor Testing Station. 31:237-242.
______ and B. J. Kaston. A list of Utah spiders, with their localities. 43:494-522.
______ and Morris A. Goates. Mites from mammals at the Nevada Test Site. 24:71-73.
______ and Stanley Mulaik. Two isopods of the Nevada Test Site. 25:43-47.
______ and Martin H. Muma. Solpugids of the National Reactor Testing Station, Idaho. 31:164-168.
______ and Vasco M. Tanner. Beetles from the environs of Lake Powell in southern Utah and northern Arizona. 39:89-96.
______, D. Elmer Johnson, and D Elden Beck. A list of some beeflies of the Nevada Test Site. 25:5-11.
______. *See* Anderson, Arthur O. 24:93-101.
______. *See* Beck, D Elden 26:9-16; 27:67-78; 28:132-141.
______. *See* Johnson, John D. 32:154-170.
______. *See* Tipton, Vernon J. 11:105-114.
Allred, Kelly W. New Mexico grass types and a selected bibliography of New Mexico grass taxonomy. 50:73-82.
______. The plant family Gentianaceae in Utah. 36:483-495.
Allred, Kelly Wayne. *Paspalum distichum* L. var. *indutum* Shinners (Poaceae). 42:101-104.
Amy, Penny S. *See* Hall, Deborah A. 50:289-294.
Andersen, Ferron L. and M. John Ramsay. Field clinic procedures for diagnosis of *Echinococcus granulosus* in dogs. 47:207-219.
______ and Paul R. Roper. Computerized reduction of meteorologic measurements from irrigated and nonirrigated plots in central Utah. 35:203-230.
______, John R. Crellin, Craig R. Nichols, and Peter M. Schantz. Evaluation of a program to control hydatid disease in central Utah. 43:65-72.
______, Keith H. Hoopes, and J. Carl Fox. The efficacy of Haloxon and Thiabendazole as anthelmintics against gastro-intestinal nematodes in sheep. 29:35-41.
______, Lauritz A. Jensen, H. Dennis McCurdy, and Craig R. Nichols. Three-year surveillance for cestode infections in sheep dogs in central Utah. 46:208-216.
______. *See* Bullick, Graham R. 38:369-378.
______. *See* Fox, J. Carl 30:131-145.
______. *See* Jensen, Lauritz A. 42:65-66; 42:351-352.
______. *See* Sawyer, Thomas W. 36:471-474.
______. *See* Schantz, Peter M. 40:216-220.
Andersen, W. R. *See* Davis, Tim D. 45:520-526.
Andersen, William R. and Jack D. Brotherson. Ribulose diphosphate carboxylase activities in cold-resistant common mallow, *Malva neglecta* Wallr., and a cold-sensitive tomato, *Lycopersicon esculentum* L., Ace 55 var. 40:121-126.
______. *See* Coleman, Craig E. 46:573-576.
Anderson, Arthur O. and Dorald M. Allred. Kangaroo rat burrows at the Nevada Test Site. 24:93-101.
Anderson, B. B. and F. H. Emmerson. The rattlesnake *Crotalus atrox* in southern Nevada. 30:107.
Anderson, Christine Minton. Cattail decline at Farmington Bay Waterfowl Management Area. 37:24-34.
Anderson, Dean A. Dragon flies feed on termites. 7:29.
Anderson, Gary A. *See* Williams, Jack E. 50:243-248.
Anderson, Loran C. *Chrysothamnus nauseosus* ssp. *iridis* (Asteraceae): a new endemic from Utah. 41:311-313.
______. *Chrysothamnus nauseosus* ssp. *uintahensis*: a stabilized hybrid. 44:416-420.
______. *Haplopappus alpinus* (Asteraceae): a new species from Nevada. 40:73-77.
______. *Haplopappus crispus* and *H. zionis* (Asteraceae): New species from Utah. 43:358-364.
______. Identity of narrow-leaved *Chrysothamnus viscidiflorus* (Asteraceae). 40:117-120.
______. A new species of fossil *Chrysothamnus* (Asteraceae) from New Mexico. 40:351-352.
______ and Phillip S. Weberg. The anatomy and taxonomy of *Vanclevea* (Asteraceae). 34:151-160.
Anderson, Russell D. The Dytiscidae (Coleoptera) of Utah: keys, original citation, types and Utah distribution. 22:54-75.
Anderson, Stanley H., Wayne A. Hubert, Craig Patterson, Alan J. Redder, and David Duvall. Distribution of vertebrates of the Bighorn Canyon National Recreation Area. 47:512-521.
______. *See* Cochran, Jean F. 47:459-466.
______. *See* Gutzwiller, Kevin J. 46:358-360.
______. *See* MacLaren, Patricia A. 48:548-553.
______. *See* Ward, John P. 49:449-455.
Andre, John B. and James A. MacMahon. Reproduction in three sympatric lizard species from west-central Utah. 40:68-72.
Angell, Raymond F. *See* Miller, Richard F. 47:349-354.

Apa, Anthony D., Daniel W. Uresk, and Raymond L. Linder. Black-tailed prairie dog populations one year after treatment with rodenticides. 50:107-113.

Armstrong, David M. Distributional patterns of mammals in Utah. 37:457-474.

______. Ecological distribution of rodents in Canyonlands National Park, Utah. 39:199-205.

Arndt, Rudolf G. *See* Medica, Philip A. 35:317-318.

______. *See* Medica, Philip A. 36:108-110.

Arthur, W. John, III. *See* Halford, Douglas K. 47:105-109.

______. *See* Reynolds, Timothy D. 46:513-527.

Arvizo, Edward R. *See* Worthington, Richard D. 33:124-128.

Ashley, John, Samuel R. Rushforth, and Jeffrey R. Johansen. Soil algae of cryptogamic crusts from the Uintah Basin, Utah, U.S.A. 45:432-442.

Asquith, Adam. Taxonomy and variation of the *Lopidea nigridia* complex of western North America (Heteroptera: Miridae: Orthotylinae). 50:135-154.

Atkins, Riley J. *See* Barkworth, Mary E. 43:561-572.

Atwood, N. Duane. The Hydrophyllaceae of Utah. 36:1-55.

______. A revision of the *Phacelia* Crenulatae group (Hydrophyllaceae) for North America. 35:127-190.

______ and Stanley L. Welsh. An *Erigeron* from Nevada and a *Penstemon* from Idaho. 48:495-498.

______ and Stanley L. Welsh. New species of *Talinum* (Portulaceae) from Utah. 45:485-487.

______, Sherel Goodrich, and Stanley L. Welsh. New *Astragalus* (Leguminosae) from the Goose Creek Drainage, Utah-Nevada. 44:263-264.

______. *See* Welsh, Stanley L. 35:327-376; 37:95-96; 38:125-179; 41:1-108.

Au, F. *See* Vollmer, A. T. 37:81-86.

Austin, Dennis D. Body composition and organ weights of the verdin (*Auriparus flaviceps*). 31:66-68.

______. Fat depth at the xiphoid process--a rapid index to deer condition. 44:178-181.

______. Plant community changes within a mature pinyon-juniper woodland. 47:96-99.

______ and W. Glen Bradley. Additional records for uncommon birds in southern Nevada. 26:41-42.

______ and W. Glen Bradley. Bird records for Clark County, Nevada. 28:61-62.

______ and Lucy Jordan. Responses of Utah deer hunters to a checking station questionnaire. 49:159-166.

______ and J. Scott Miller. Temperature-related behavior of some migrant birds in the desert. 42:232-240.

______ and Dennis D. Murphy. Zoogeography of Great Basin butterflies: patterns of distribution and differentiation. 47:186-201.

______ and Philip J. Urness. Consumption of fresh alfalfa hay by mule deer and elk. 47:100-102.

______ and Philip J. Urness. Vegetal responses and big game values after thinning regenerating lodgepole pine. 42:512-516.

______, Robert A. Riggs, Philip J. Urness, David L. Turner, and John F. Kimball. Changes in mule deer size in Utah. 49:31-35.

______, Philip J. Urness, and J. King. Late summer changes in mule deer diets with increasing use on bitterbrush rangeland. 44:572-574.

______, Philip J. Urness, and Michael L. Wolfe. The influence of predator control on two adjacent wintering deer herds. 37:101-102.

Avery, David F. and Wilmer W. Tanner. Speciation in the Fijian and Tongan iguana *Brachylophus* (Sauria, Iguanidae) with the description of a new species. 30:166-172.

______. *See* Fanghella, Charles 35:245-268.

Axler, R. P., R. M. Gersberg, and L. J. Paulson. Primary productivity in meromictic Big Soda Lake, Nevada. 38:187-192.

B

Bachman, V. C. *See* Knopf, F. L. 37:247-251.

Bagley, V. L. *See* Ralphs, M. H. 48:541-547.

Bailey, Reeve M. *See* Courtenay, Walter R., Jr. 47:523-526.

Bailie, Geoffrey L. *See* Poché, Richard M. 34:254-256.

Baird, Craig R. Field behavior and seasonal activity of the rodent bot fly, *Cuterebra tenebrosa*, in central Washington (Diptera: Cuterebridae). 34:247-253.

Baker, Edward W. *See* Tuttle, Donald M. 36:57-64.

Baker, John R. *See* Koenig, Ervon R. 31:106-108.

Baker, M. F. *See* Nichols, D. W. 35:191-202.

Baker, Marc A., Donald J. Pinkava, Bruce Parfitt, and Timothy Righetti. On *Cowania* and its intergeneric hybrids in Arizona. 44:484-486.

Baker, William L. Additions to a bibliography of Colorado vegetation description. 44:677-680.

______. A bibliography of Colorado vegetation description. 43:45-64.

______. Classification of the riparian vegetation of the montane and subalpine zones in western Colorado. 49:214-228.

______. A preliminary classification of the natural vegetation of Colorado. 44:647-676.

______. Some aspects of the presettlement vegetation of the Piceance Basin, Colorado. 43:687-699.

______ and Susan C. Kennedy. Presettlement vegetation of part of northwestern Moffat County, Colorado, described from remnants. 45:747-777.

Bakewell, George, Joseph M. Chopek, and Gary L. Burkholder. Notes on reproduction of the side-blotched lizard *Uta stansburiana stansburiana* in southwest Idaho. 43:477-482.

Bales, Frances M. and Malcolm M. Furniss. Bionomics of the cone spittlebug, *Aphrophora canadensis* (Homoptera: Cercopidae), on mugo pine in Idaho. 44:338-348.

Bamberg, S. A. *See* Vollmer, A. T. 37:81-86.

Banks, Richard C. Annotated bibliography of Nevada

ornithology since 1951. 28:49-60.
Banta, Benjamin H. and Wilmer W. Tanner. A brief historical resume of herpetological studies in the Great Basin of the western United States. Part I: The reptiles. 24:37-57.
______ and Wilmer W. Tanner. The systematics of *Crotaphytus wislizeni*, the leopard lizards (Sauria: Iguanidae), Part II: A review of the status of the Baja California peninsular populations and a description of a new subspecies from Cedros Islands. 28:183-194.
______. *See* Powers, Arnold L. 34:241-244.
______. *See* Tanner, Wilmer W. 22:116-118; 23:129-148; 26:87-135; 37:225-240.
______. *See* Tinkham, Ernest R. 34:203-206.
Barber, Delbert R. and Lawrence L. Lockard. Some helminths from mink in southwestern Montana, with a checklist of their internal parasites. 33:53-60.
Barkworth, Mary E., Douglas R. Dewey, and Riley J. Atkins. New generic concepts in the Triticeae of the Intermountain Region: key and comments. 43:561-572.
Barnby, Mark A. *See* Resh, Vincent H. 44:99-103.
Barneby, Rupert C. and Stanley L. Welsh. New species of *Astragalus* (Leguminosae) from southeastern Utah. 45:551-552.
Barnes, A. M., V. J. Tipton, and J. A. Wildie. The subfamily Anomiopsyllinae (Hystrichopsyllidae: Siphonaptera). I. A revision of the genus *Anomiopsyllus* Baker. 37:138-206.
Barnes, Claude T. The hawthorn, *Crataegus colorado*, a new record for Utah. 4:55.
______. The plant clear-eye or see-bright, a new record for Utah. 6:128.
Barnes, James R., J. V. McArthur, and C. E. Cushing. Effect of excluding shredders on leaf litter decomposition in two streams. 46:204-207.
______. *See* McArthur, J. Vaun 45:117-123.
______. *See* Ng, David 46:310-315.
______. *See* Winger, Parley V. 32:211-219.
Barnes, Sarah J. *See* Brotherson, Jack D. 44:299-309.
Barnum, Andrew H. Notes on *Amblycheila utahensis* Tanner (Coleoptera: Cicindelidae). 20:79-80.
______. The taxonomy of Utah Orthoptera. 14:39-60.
______. Tribute to Dr. Vasco M. Tanner. 30:211-212.
Barr, William F. The Buprestidae and Cleridae of the Nevada Test Site (Coleoptera). 29:11-19.
______. A new subspecies of *Enoclerus* from the Great Basin region of the western United States (Coleoptera: Cleridae). 7:21-22.
______ and Richard L. Penrose. Notes on the distribution and bionomics of some Idaho Cerambycidae (Coleoptera). 29:88-95.
______. *See* Stafford, Michael P. 46:287-293.
Bartmann, Richard M. Growth rates of mule deer fetuses under different winter conditions. 46:245-248.
Bartos, Dale L. and James E. Lester. Effects of 2,4-D on a *Populus tremuloides* community in the western United States--22 years after treatment. 44:459-467.
Bateman, Lucinda. Comparative floral biology of *Penstemon eatonii* and *Penstemon cyananthus* in central Utah: a preliminary study. 40:268-272.
Baugh, Thomas M. Adapting Salt Creek pupfish (*Cyprinodon salinus*) to fresh water. 41:341-342.
______. Spawning of the least chub (*Iotichthys phlegethontis*). 40:139-140.
______ and Bruce G. Brown. Field observations on the response of the Railroad Valley springfish (*Crenichthys nevadae*) to temperature. 40:359-360.
______ and James E. Deacon. Daily and yearly movement of the Devil's Hole pupfish *Cyprinodon diabolis* Wales in Devil's Hole, Nevada. 43:592-596.
______, Michael A. Nelson, and Floyd Simpson. A description of Timpie Springs, Utah, with a preliminary survey of the aquatic macrobiota. 42:77-80.
______, John W. Pedretti, and James E. Deacon. Status and distribution of the Fish Creek Springs tui chub, *Gila bicolor euchila*. 46:441-444.
Baumann, Richard W. Nearctic stonefly genera as indicators of ecological parameters (Plecoptera: Insecta). 39:241-244.
______. Studies on Utah stoneflies (Plecoptera). 33:91-108.
______ and Bill P. Stark. *Hesperoperla hoguei*, a new species of stonefly from California (Plecoptera: Perlidae). 40:63-67.
______. *See* Jacobi, Gerald Z. 43:585-591.
______. *See* Nelson, C. Riley. 49:289-363.
______. *See* Stark, Bill P. 38:97-114; 46:383-397.
Bayn, Robert L., Jr. *See* Schimpf, David J. 43:573-578.
Beard, James M. *See* Tyus, Harold M. 50:33-39.
Beatley, Janice C. *See* Reveal, James L. 34:230.
Beatty, Joseph J. *See* Whitaker, John O., Jr. 46:228-240.
Bechtel, R. C. *See* Rust, R. W. 43:403-408.
Beck, D Elden. California Gull, a comparative plumage study. 4:57-61.
______. A land planarian collected in Utah. 12:62.
______. Life history notes on the California Gull, No. 1. 3:91-108.
______. Notes on the occurrence of gulls at Utah Lake. 3:54.
______. Siphonaptera (fleas) of Mesa Verde National Park, Montezuma, Colorado. 26:76-78.
______ and Dorald M. Allred. Faunistic inventory--BYU ecological studies at the Nevada Test Site. 28:132-141.
______ and Dorald M. Allred. Tingidae, Neididae (Berytidae) and Pentatomidae of the Nevada Test Site. 26:9-16.
______, Dorald M. Allred, and William J. Despain. Predaceous-scavenger ants in Utah. 27:67-78.
______. *See* Allred, Dorald M. 13:87-90; 25:5-11; 25:77-79; 27:11-25.
______. *See* Brennan, James M. 15:1-26

______. *See* Mohr, Carol O. 24:1-6.
______. *See* Tanner, Vasco M. 3:55-57.
Becker, Jonathan J. Fossil birds of the Oreana local fauna (Blancan), Owyhee County, Idaho. 46:763-768.
Beckham, G. B. *See* Wallace, Richard L. 44:324-326.
Bedwell, Stephen F. New evidence for the presence of turkey in the early postglacial period of the northern Great Basin. 31:48-49.
Bee, James W. Vasco M. Tanner--a diversified career. 30:216-217.
Bee, Robert G. and John Hutchings. Breeding records of Utah birds. 3:61-85.
Beetle, Dorothy E. Checklist of recent Mollusca of Wyoming, USA. 49:637-645.
Behan, Barbara and Bruce L. Welch. Winter nutritive content of black sagebrush (*Artemisia nova*) grown in a uniform garden. 46:161-165.
Behle, William H. In memoriam: Seville Flowers (1900-1968). 44:210-222.
______. In memoriam: William Wallace Newby (1902-1977). 45:443-444.
______. Significant bird records from Utah. 33:243-245.
______. Water birds observed at Rock Island, Utah Lake, in 1932. 6:127-128.
______ and Jon Ghiselin. Additional data on the birds of the Uinta mountains and basin of northeastern Utah. 18:1-22.
Belk, Mark C., Clyde L. Pritchett, and H. Duane Smith. Patterns of microhabitat use of *Sorex monticolus* in summer. 50:387-389.
______. *See* Robey, Edward H., Jr. 47:488-496.
Benson, Brock. *See* Ralphs, Michael H. 49:419-424.
Benton, Bob. *See* Hovingh, Peter 45:22-30.
Berger, Randy. *See* Pekins, Peter J. 49:229-232.
Berna, Howard J. Observations on the dwarf shrew (*Sorex nanus*) in northern Arizona. 50:161-165.
Berner, Kevin L. *See* Findholt, Scott L. 48:290-297.
Best, Troy L. and A. L. Gennaro. Food habits of the western whiptail lizard (*Cnemidophorus tigris*) in southeastern New Mexico. 45:527-534.
Betancourt, Julio L. Late Quaternary plant zonation and climate in southeastern Utah. 44:1-35.
Bhat, R. B. *See* Hegerhorst, D. F. 48:1-8.
Bienek, Gerhard K. and Albert W. Grundmann. Burrowing habits of two subspecies of *Dipodomys merriami* in California and Utah. 31:190-192.
Biggam, R. C. and M. A. Brusven. Gerridae (water striders) of Idaho (Heteroptera). 49:259-274.
Bjerregaard, R. S., N. E. West, M. M. Caldwell, and H. F. Maryland. Standing crops and dynamics of phytomass and minerals in two salt desert shrub communities. 44:327-337.
Black, Andrew H. *See* Black, Jeffrey H. 47:344.
Black, Hal L. Differential utilization of bat boxes by house wrens (*Troglodytes aedon*). 43:456.
______ and Clayton M. White. High localized bird mortality as a function of high insect populations. 28:200.
______. *See* Zou, Jiping. 49:435-448.
Black, Jeffrey Howard. Observations on courtship behavior of the desert tortoise. 36:467-470.
______ and Andrew H. Black. Western painted turtle in Grant County, Oregon. 47:344.
______ and Royal Bruce Brunson. Breeding behavior of the boreal toad, *Bufo boreas boreas* (Baird and Girard), in western Montana. 31:109-113.
______ and Robert M. Storm. Notes on the herpetology of Grant County, Oregon. 30:9-12.
Black, Richard D. *See* Brotherson, Jack D. 46:348-357.
Blackburn, Del F. Courtship behavior among white-tailed and black-tailed jackrabbits. 33:203-204.
Blackburn, Wilbert H. and Karl Wood. Influence of soil frost on infiltration of shrub coppice dune and dune interspace soils in southeastern Nevada. 50:41-46.
Blain, R. Leonard. *See* Daniel, Joseph C., Jr. 19:37-42.
Blake, Elizabeth A. and Michael R. Wagner. Foliage age as a factor in food utilization by the western spruce budworm, *Choristoneura occidentalis*. 46:169-172.
______. *See* Mathiasen, Robert L. 46:277-280.
______. *See* Mathiasen, Robert L. 47:467-472.
Blake, John G. Avifauna of the Mt. Dellenbaugh region, Shivwits Plateau, Arizona. 41:259-268.
Blaustein, Andrew R. and Arthur C. Risser, Jr. Dominance relationships of the dark kangaroo mouse (*Microdipodops megacephalus*) and the little pocket mouse (*Perognathus longimembris*) in captivity. 34:312-316.
Blazzard, John E. Some memories and impressions of my association with Vasco M. Tanner. 30:207-208.
Bleich, Vernon C. and Andrew M. Pauli. Additional records of the spotted bat (*Euderma maculatum*) from California. 48:563.
______ and Orlando A. Schwartz. Water balance and fluid consumption in the southern grasshopper mouse, *Onychomys torridus*. 35:62-64.
Blinn, Dean W. and Milton W. Sanderson. Aquatic insects in Montezuma Well, Arizona, USA: a travertine spring mound with high alkalinity and dissolved carbon dioxide. 49:85-88.
Bloss, Deborah Ann and Jack D. Brotherson. Vegetation response to a moisture gradient on an ephemeral stream in central Arizona. 39:161-176.
Bock, Carl E. and Larry W. Lepthien. Correction for: Carl E. Bock and Larry W. Lepthien, distribution and abundance of the Black-billed Magpie (*Pica pica*) in North America. Great Basin Naturalist 35(3):269-272. 36:111.
______ and Larry W. Lepthien. Distribution and abundance of the Black-billed Magpie (*Pica pica*) in North America. 35:269-272.
Bohman, Verle R. *See* Poole, Stephen C. 49:201-213.
Bond, Carl E. *See* Williams, Jack E. 43:409-420.
Booth, Gary M. *See* Stewart, David A. 39:129-132.
Borchert, Mark. *See* Owings, Donald H. 35:402-404.
Bornholdt, Dave. *See* Hovingh, Peter 45:22-30.

Bourgeron, P. S., L. D. Engelking, J. S. Tuhy, and J. D. Brotherson. Bibliography of Nevada and Utah vegetation description. 50:209-242.

______, A. M. Kratz, T. Weaver, and N. Weidman. Bibliography of Montana vegetation description. 48:301-323.

Bowers, Janice E. Local floras of the Southwest, 1920-1980: an annotated bibliography. 42:105-112.

Bowers, Michael A. Insular biogeography of mammals in the Great Salt Lake. 42:589-596.

Bozek, Michael A. Orientation of zooplankton to the oxycline in Big Soda Lake, Nevada. 49:535-539.

Bradley, W. Glen and Charles G. Hansen. A probable record of the white-tailed deer in Nevada. 28:199.

______. *See* Austin, George T. 26:41-42; 28:61-62.

Bragg, Arthur N. The Amphibia of Greer County, Oklahoma. 15:27-31.

______. Observations on the ecology and natural history of Anura XV. The hylids and microhylids in Oklahoma. 4:62-80.

______. Some observations on Amphibia at and near Las Vegas, New Mexico. 2:109-117.

______. Some salientian adaptations. 7:11-15.

______ and Harold A. Dundee. Reptiles collected in the vicinity of Las Vegas, New Mexico. 9:55-57.

______ and W. F. Hudson. New county records of Salientia and a summary of known distribution of Caudata in Oklahoma. 11:87-90.

______ and Charles Clinton Smith. Observations on the ecology and natural history of Anura IX. Notes on breeding behavior in Oklahoma. 3:33-50.

Brame, Arden H., Jr. *See* Tanner, Wilmer W. 21:23-26.

Branham, Joseph M., Arden R. Gaufin, and Robbin L. Traver. Growth of Plecoptera (stonefly) nymphs at constant, abnormally high temperatures. 35:51-61.

Braun, Clait E. *See* Olsen, O. Wilford 36:445-457.

Brennan, J. M. *See* Goff, M. L. 37:501-509.

Brennan, James M. and D Elden Beck. The chiggers of Utah (Acarina: Trombiculidae). 15:1-26.

Bres, Mimi. *See* Sigler, William F. 45:571-603.

Brienholt, Craig and Richard A. Heckmann. Parasites from two species of suckers (Catostomidae) from southern Utah. 40:149-156.

Briggs, George M. and James A. MacMahon. Alpine and subalpine wetland plant communities of the Uinta Mountains, Utah. 43:523-530.

______ and James A. MacMahon. Structure of alpine plant communities near King's Peak, Uinta Mountains, Utah. 42:50-59.

Bright, Donald E. New species and new records of North American *Pityophthorus* (Coleoptera: Scolytidae), Part V: The Juglandis group. 45:476-482.

______. New species and new records of North American *Pityophthorus* (Coleoptera: Scolytidae), Part VI: The Lautus Group. 46:641-645.

______. New species and new records of North American *Pityophthorus* (Coleoptera: Scolytidae). Part VII. 46:679-684.

______. New species and records of North American *Pityophthorus* (Coleoptera: Scolytidae), Part IV: The Scriptor group. 45:467-475.

______. New synonymy, new combinations, and new species of North American *Pityophthorus* (Coleoptera: Scolytidae), Part II. 36:425-444.

______. New synonymy, new species, and taxonomic notes of North American *Pityophthorus* (Coleoptera: Scolytidae), Part III. 38:71-84.

Brinton, Elias P. and Glen M. Kohls. New distributional and host data for the tick *Dermacentor hunteri* Bishopp. 23:166.

Brinton, Elias P. *See* Mohr, Carol O. 24:1-6.

Brittell, J. David. *See* Knick, Steven T. 44:70-74.

Britton, Carlton M., Guy R. McPherson, and Forrest A. Sneva. Effects of burning and clipping on five bunchgrasses in eastern Oregon. 50:115-120.

Broome, Rose C. A new variety of *Centaurium namophilum* (Gentianaceae) from the Great Basin. 41:192-197.

Brothers, Donald R. First record of *Patapius spinosus* in Idaho and Nevada (Hemiptera: Leptopodidae). 39:195-196.

Brothers, Timothy. *See* Lee, M. A. B. 41:370-376.

Brotherson, Jack D. Plant community zonation in response to soil gradients in a saline meadow near Utah Lake, Utah County, Utah. 47:322-333.

______. Species composition, distribution, and phytosociology of Kalsow Prairie, a mesic tall grass prairie in Iowa. 43:137-167.

______. Vegetation of the mima mounds of Kalsow Prairie, Iowa. 42:246-261.

______. Zonation patterns in the potholes of Kalsow Prairie, Iowa. 40:372-384.

______ and Sarah J. Barnes. Habitat relationships of *Glaux maritima* in central Utah. 44:299-309.

______ and Karen J. Brotherson. Ecological and community relationships of *Eriogonum corymbosum* (Polygonaceae) in the Uinta Basin, Utah. 39:177-191.

______ and W. Todd Brotherson. Grazing impacts on sagebrush communities of central Utah. 41:335-340.

______ and William J. Masslich. Vegetation patterns in relation to slope position in the Castle Cliffs area of southern Utah. 45:535-541.

______ and Kevin P. Price. Naturalization and habitat relationships of bitter nightshade (*Solanum dulcamara*) in central Utah. 44:317-323.

______ and Samuel R. Rushforth. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. 43:73-78.

______ and Samuel R. Rushforth. Invasion and stabilization of recent beaches by salt grass (*Distichlis spicata*) at Mono Lake, Mono County, California. 45:542-545.

______ and Samuel R. Rushforth. Zonation patterns in the vascular plant communities of Benton Hot

Springs, Mono County, California. 47:583-591.

______ and Von Winkel. Habitat relationships of saltcedar (*Tamarix ramosissima*) in central Utah. 46:535-541.

______, William E. Evenson, Samuel R. Rushforth, John Fairchild, and Jeffrey R. Johansen. Spatial patterns of plant communities and differential weathering in Navajo National Monument, Arizona. 45:1-13.

______, G. Nebeker, M. Skougard, and J. Fairchild. Plants of Navajo National Monument. 38:19-30.

______, K. P. Price, and L. O'Rourke. Age in relationship to stem circumference and stem diameter in cliffrose (*Cowania mexicana* var. *stansburiana*) in central Utah. 47:334-338.

______, Lars L. Rasmussen, and Richard D. Black. Comparative habitat and community relationships of *Atriplex confertifolia* and *Sarcobatus vermiculatus* in central Utah. 46:348-357.

______, Lee A. Szyska, and William E. Evenson. Bird community composition in relation to habitat and season in Betatakin Canyon, Navajo National Monument, Arizona. 41:298-309.

______, Lee A. Szyska, and William E. Evenson. Poisonous plants of Utah. 40:229-253.

______. *See* Andersen, William R. 40:121-126.

______. *See* Bloss, Deborah Ann 39:161-176.

______. *See* Bourgeron, P. S. 50:209-242.

______. *See* Callison, James 45:321-326.

______. *See* Cedarleaf, Joy D. 42:91-95.

______. *See* Christensen, E. M. 39:263-266.

______. *See* Evenson, William E. 40:167-174.

______. *See* Grimes, Judith A. 44:36-48.

______. *See* Jatkar, Shobha A. 39:15-43.

______. *See* Johansen, Jeffrey R. 41:433-439.

______. *See* Masslich, William J. 48:250-262.

______. *See* Morden, C. 46:140-147.

______. *See* Moretti, Miles O. 42:81-90.

______. *See* Price, K. P. 47:132-151.

______. *See* Rasmussen, Lars L. 46:148-156.

______. *See* Shupe, J. B. 45:141-149.

______. *See* Skougard, Michael G. 39:44-58.

______. *See* Skousen, J. 46:508-512.

______. *See* Skousen, Jeffrey G. 42:562-566.

______. *See* Squires, Lorin E. 39:245-252.

______. *See* Webb, G. Merrill 48:274-279; 48:512-529.

______. *See* Whiting, Mark C. 38:31-41.

______. *See* Wood, Alan K. 41:457-460; 41:274-250.

Brotherson, Karen J. *See* Brotherson, Jack D. 39:177-191.

Brotherson, W. Todd. *See* Brotherson, Jack D. 41:335-340.

Brown, Barbara A., John O. Whitaker, Thomas W. French, and Chris Maser. Note on food habits of the Screech Owl and the Burrowing Owl of southeastern Oregon. 46:421-426.

Brown, Bruce G. *See* Baugh, Thomas M. 40:359-360.

Brown, David E. *See* Davis, Russell. 49:425-434.

Brown, John A. *See* Young, James A. 46:1-21.

Brown, Walter C. and Vasco M. Tanner. Rediscovery of the genus *Pseudogekko* with description of a new species from the Solomon Islands. 9:41-45.

Browning, M. Ralph. Geographic variation in *Contopus sordidulus* and *C. virens* north of Mexico. 37:453-456.

Bruhn, Arthur F. The external male genitalia of some Rhynchophora. 8:1-35.

Brunson, John T., Richard N. Seaman, and Donald J. Nash. Interpopulational variation of blood proteins in pika (*Ochotona princeps saxatilis*). 37:77-80.

Brunson, Royal Bruce. *See* Black, Jeffrey Howard 31:109-113.

Brusven, M. A. *See* Biggam, R. C. 49:259-274.

Brusven, Merlyn A. *See* Hornig, C. Evan 46:33-38.

______. *See* Meehan, William R. 47:22-31.

Bryan, James A. *See* Lanner, Ronald M. 40:190-192; 41:476-477.

Buchanan, Bruce A., K. T. Harper, and Neil C. Frischknecht. Allelopathic effects of bur buttercup tissue on germination and growth of various grasses and forbs *in vitro* and in soil. 38:90-96.

Buchanan, Hayle and Robert Graybosch. Revised checklist of the vascular plants of Bryce Canyon National Park, Utah. 41:109-120.

______. *See* Graybosch, Robert A. 43:701-712.

Buchholz, Todd D. *See* McComb, William C. 50:273-281.

Bullick, Graham R. and Ferron L. Andersen. Effect of irrigation on survival of third-stage *Haemonchus contortus* larvae (Nematoda: Trichostrongylidae). 38:369-378.

Bullock, Robert E. Cannibalism in captive rattlesnakes. 31:49-50.

Bunderson, E. D., D. J. Weber, and D. L. Nelson. Diseases associated with *Juniperus osteosperma* and a model for predicting their occurrence with environmental site factors. 46:427-440.

Bunn, Richard L. Breeding records for Clark's Grebe in Colorado and Nevada. 46:581-582.

Bunting, Stephen C. *See* Mosley, Jeffrey C. 49:241-248.

______. *See* Smith, Stuart D. 47:299-307.

Burke, Thomas E. *See* Marsh, Paul C. 49:387-389.

Burkholder, Gary L. *See* Bakewell, George 43:477-482.

Burns, James A., Dennis L. Flath, and Tim W. Clark. On the structure and function of white-tailed prairie dog burrows. 49:517-524.

Burns, Steven J. and Richard E. Terry. Blockage and recovery of nitrification in soils exposed to acetylene. 46:316-320.

Burton, Sheril D. *See* Rushforth, Samuel R. 40:98-100.

Bushnell, John H., Susan Q. Foster, and Bruce M. Wahle. Annotated inventory of invertebrate populations of an alpine lake and stream chain in Colorado. 47:500-511.

Butler, David R. Vegetational and geomorphic change on snow avalanche paths, Glacier National Park, Montana, USA. 45:313-317.

______. *See* Malanson, George P. 44:453-458.

C

Caire, William. *See* Finley, Robert B. 43:554-560.

Calder, J. Hamilton. Vasco M. Tanner--a dedicated public servant. 30:197-199.

Caldwell, Bruce A. *See* Li, C. Y. 46:411-414.

Caldwell, M. M. *See* Bjerregaard, R. S. 44:327-337.

Call, C. A. and C. M. McKell. Field establishment of fourwing saltbush in processed oil shale and disturbed native soil as influenced by vesicular-arbuscular mycorrhizae. 44:363-371.

Callison, James and Jack D. Brotherson. Habitat relationships of the blackbrush community (*Coleogyne ramosissima*) of southwestern Utah. 45:321-326.

Cameron, D. E. and M. J. Jenkins. Engelmann spruce cone losses caused by insects in northern Utah in a year of low cone production. 48:508-511.

Campbell, R. B. *See* McDonough, W. T. 35:325-326.

Campbell, Thomas M., III and Tim W. Clark. Short-term effects of logging on red-backed voles and deer mice. 40:183-189.

______, Tim W. Clark, and Craig R. Groves. First record of pygmy rabbits (*Brachylagus idahoensis*) in Wyoming. 42:100.

______. *See* Clark, Tim W. 41:360-361; 42:572-582; 43:438-440; 49:587-596.

Campbell, W. F. *See* Rechel, E. A. 38:456-462.

Campos, E. G. Deer mouse, *Peromyscus maniculatus*, and associated rodent fleas (Siphonaptera) in the arctic-alpine life zone of Rocky Mountain National Park, Colorado. 43:168-174.

______. *See* Eads, R. B. 42:241-245.

Carlin, K. D. *See* Schmid, J. M. 44:575-578.

Carpenter, Alan T. *See* Neely, Elizabeth E. 46:728-735.

Carraway, Leslie N. *See* Verts, B. J. 41:167-175.

Carroll, T. *See* Heckmann, R. A. 45:255-265.

Carter, James L. *See* Leland, Harry V. 46:595-611.

Carter, John G. *See* Lamarra, Vincent A. 45:127-140; 46:690-705.

Carter-Lovejoy, Steven H. The relation between species numbers and island characteristics for habitat islands in a volcanic landscape. 42:113-119.

Casey, Denise E. *See* Clark, Tim W. 42:572-582.

Casey, Osborne. *See* Nelson, Rodger L. 47:480-487.

Cates, Rex G. *See* Masslich, William J. 48:250-262.

Cather, Mary R. and Arden R. Gaufin. Life history and ecology of *Megarcys signata* (Plecoptera: Perlodidae), Mill Creek, Wasatch Mountains, Utah. 35:39-48.

______, Bill P. Stark, and Arden R. Gaufin. Records of stoneflies (Plecoptera) from Nevada. 35:49-50.

Cazier, Mont A. New American *Diplotaxis* (Coleoptera-Scarabaeidae). 1:127-137.

______. The southwestern research station of the American Museum of Natural History. 14:91.

Cedarleaf, Joy D., S. Dick Worthen, and Jack D. Brotherson. Weather conditions in early summer and their effects on September Blue Grouse (*Dendragapus obscurus*) harvest. 42:91-95.

Chamberlain, Roy W. Four new species of *Collembola*. 4:39-48.

Chamberlin, Ralph V. Further records and descriptions of American millipeds. 12:13-34.

______. Geophiloid chilopods of the Hawaiian and other oceanic islands of the Pacific. 13:75-85.

______. A new genus and species in the chilopod family Tampiyidae. 25:39-42.

______. On eight new southern millipeds. 11:19-26.

______. On five new American lithobiid centipeds. 11:115-118.

______. Records of American millipeds and centipeds collected by Dr. D. Elden Beck in 1950. 11:27-35.

______. Scolopendrid chilopods of the northern Andes Region taken on the California Academy South American Expedition of 1954-1955. 17:30-41.

Chandler, Harry P. New species of *Coleoptera* from Utah (Omophronidae and Dytiscidae). 2:99-104.

Chapman, Harold C. *See* Drake, Carl J. 13:9-11

Chapman, Joseph A. *See* Cramer, Kenneth L. 50:283-285; 50:361-365.

Chatterley, L. Matthew, Blaine T. Welsh, and Stanley L. Welsh. Preliminary index of authors of Utah plant names. 42:385-394.

______. *See* Welsh, Stanley L. 45:173-236.

Ching, H. L. *See* Heckmann, R. A. 47:259-275.

Chitaley, Shya. *See* Nambudiri, E. M. V. 47:527-535.

Cholewa, Anita F. and Douglass M. Henderson. A survey and assessment of the rare vascular plants of the Idaho National Engineering Laboratory site. 44:140-144.

Chopek, Joseph M. *See* Bakewell, George 43:477-482.

Christensen, E. M. and J. D. Brotherson. Decreases of juniper woodland in the Utah and Salt Lake valleys since settlement. 39:263-266.

Christensen, Earl M. Bibliography of Utah aquatic biology, No. II. 22:32-53.

______. The recent naturalization of Siberian elm (*Ulmus pumila* L.) in Utah. 24:103-106.

______. The root system of bigtooth maple. 22:114-115.

Christiansen, Tim A., Jeffrey A. Lockwood, and Jeff Powell. Arthropod community dynamics in undisturbed and intensively managed mountain brush habitats. 49:570-586.

______, Jeffrey A. Lockwood, and Jeff Powell. Effects of arthropods on root:shoot ratio and biomass production in undisturbed and modified mountain shrub habitats. 49:456-460.

______, Jeffrey A. Lockwood, and Jeff Powell. Litter decomposition by arthropods in undisturbed and intensively managed mountain brush habitats. 49:562-569.

______, Jeffrey A. Lockwood, and Jeff Powell. Mediation of nutrient cycling by arthropods in unmanaged and intensively managed mountain brush habitats. 49:134-139.

Cincotta, Richard P. Note on mound architecture of the black-tailed prairie dog. 49:621-623.

______, D. W. Uresk, and R. M. Hansen. Demography of black-tailed prairie dog populations reoccupying sites treated with rodenticide. 47:339-343.

Clark, Cynthia J. *See* Clark, William H. 49:36-37.

Clark, Shawn M. A revision of the genus *Microrhopala* (Coleoptera: Chrysomelidae) in America north of Mexico. 43:597-618.

Clark, Stephen L. A new combination in *Penstemon* (Scrophulariaceae). 35:434.

______. A new status for *Penstemon cyananthus* Hook. ssp. *subglaber* Pennell (Scrophulariaceae). 37:100.

______. A new status for *Penstemon cyananthus* Hook. ssp. *subglaber* Pennell (Scrophulariaceae). 37:258.

______ and Robert Graybosch. *Montia linearis* (Portulacaceae): a new record for Utah. 41:269.

Clark, Tim W. Local distribution and interspecies interactions in microtines, Grand Teton National Park, Wyoming. 33:205-217.

______. Notes on white-tailed prairie dog (*Cynomys leucurus*) burrows. 31:115-124.

______. Preliminary mammal survey of Fossil Butte National Monument, Wyoming. 37:91-94.

______. Richardson's ground squirrel (*Spermophilus richardsonii*) in the Laramie Basin, Wyoming. 30:55-70.

______. Some spatial and behavioral features of the thirteen-lined ground squirrel. 41:243-246.

______ and Thomas M. Campbell III. Additional black-footed ferret (*Mustela nigripes*) reports from Wyoming. 41:360-361.

______ and Thomas M. Campbell III. A small carnivore survey technique. 43:438-440.

______, Thomas M. Campbell III, and Tedd N. Hauptman. Demographic characteristics of American marten populations in Jackson Hole, Wyoming. 49:587-596.

______, Thomas M. Campbell III, David G. Socha, and Denise E. Casey. Prairie dog colony attributes and associated vertebrate species. 42:572-582.

______. *See* Burns, James A. 49:517-524.

______. *See* Campbell, Thomas M., III 40:183-189; 42:100.

______. *See* Korhel, Art H. 41:461-464.

Clark, William A. *See* O'Farrell, Michael J. 44:428-430.

Clark, William H. First record of *Climacia californica* (Neuroptera: Sisyridae) and its host sponge, *Ephydatia mulleri* (Porifera: spongillidae), from Idaho with water quality relationships. 45:391-394.

______ and Cynthia J. Clark. White-tailed prairie dog (*Cynomys leucurus* Merriam) diggings in western harvester ant, *Pogonomyrmex occidentalis* (Cresson), mounds. 49:36-37.

______ and Peter L. Comanor. Flights of the western thatching ant, *Formica obscuripes* Forel, in Nevada (Hymenoptera: Formicidae). 32:202-207.

Clark, William R. and Frederic H. Wagner. Role of livestock and black-tailed jackrabbits in changing abundance of *Kochia americana*. 44:635-646.

Clary, Warren P. Variation in leaf anatomy and Co_2 assimilation in *Sitanion hystrix* ecotypes. 39:427-432.

______, Peter F. Ffolliott, and Frederic R. Larson. Producer-consumer biomass in montane forests on the Arizona Mogollon Plateau. 44:627-634.

Clubb, Robert. *See* Gaufin, Arden R. 34:45-59.

Cochran, Jean F. and Stanley H. Anderson. Comparison of habitat attributes at sites of stable and declining long-billed curlew populations. 47:459-466.

Cochran, Philip A. *See* Somma, Louis A. 49:525-534.

Coffeen, M. P. *See* Pritchett, C. L. 47:231-233.

Coffey, Marvin D. A study of some Rocky Mountain spotted fever vectors and their hosts in Utah. 14:31-37.

Coggins, Victor. *See* Crawford, John A. 46:745-748.

Cole, Arthur C. *See* Allred, Dorald M. 31:237-242; 39:97-102.

Cole, David N. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. 50:321-325.

Coleman, Bruce A. *See* Heckmann, Richard A. 41:201-206; 47:355-372.

Coleman, Craig E. and William R. Andersen. Chloroplast ultrastructure in the desert shrub *Chrysothamnus nauseosus* ssp. *albicaulis*. 46:573-576.

Collins, Ellen I. *See* Lichvar, Robert W. 45:734-746.

Collins, Nicholas C. and Gray Stirling. Relationships among total dissolved solids, conductivity, and osmosity for five *Artemia* habitats (Anostraca: Artemiidae). 40:131-138.

Collins, Patrick D., Kimball T. Harper, and Burton K. Pendleton. Comparative life history and floral characteristics of desert and mountain floras in Utah. 43:385-393.

Comanor, Peter L. *See* Clark, William H. 32:202-207.

Connelly, John W. *See* Reynolds, Timothy D. 46:513-527.

Connolly, Patrick J. *See* Wallace, Richard L. 44:324-326.

Cook, A. Gaylon. Birds of the desert region of Uintah County, Utah. 44:584-620.

Cooper, James J. Age, growth, and food habits of tui chub, *Gila bicolor*, in Walker Lake, Nevada. 45:784-788.

______. Observations on the reproduction and embryology of the Lahontan tui chub, *Gila bicolor*, in Walker Lake, Nevada. 42:60-64.

Cottam, Clarence. Vasco M. Tanner--a great teacher. 30:200-202.

______, Cecil S. Williams, and Clarence A. Sooter. Some unusual winter visitors or late migrants to the Bear River Marshes, Utah. 3:51-53.

Cottam, Walter P. Vasco M. Tanner--a pioneer in

conservation. 30:203-204.
Courtenay, Walter R., Jr. and James E. Deacon. Status of introduced fishes in certain spring systems in southern Nevada. 42:361-366.
______, C. Richard Robins, Reeve M. Bailey, and James E. Deacon. Records of exotic fishes from Idaho and Wyoming. 47:523-526.
Cowgill, Lari M. *See* Sawyer, Thomas W. 36:471-474.
Cox, Darla G. *See* Cox, George W. 34:60-70.
Cox, Douglas C. and Wilmer W. Tanner. Hyobranchial apparatus of the Cryptobranchoidea (Amphibia). 49:482-490.
______ and Wilmer W. Tanner. Osteology and myology of the head and neck regions of *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma* (Reptilia: Iguanidae). 37:35-56.
______. *See* Tanner, Wilmer W. 41:314-316.
Cox, George W. Form and dispersion of Mima mounds in relation to slope steepness and aspect on the Columbia Plateau. 50:21-31.
______ and Darla G. Cox. Substrate color matching in the grasshopper, *Circotettix rabula* (Orthoptera: Acrididae). 34:60-70.
______, Christopher G. Gakahu, and Douglas W. Allen. Small-stone content of Mima mounds of the Columbia Plateau and Rocky Mountain regions: implications for mound origin. 47:609-619.
Cox, Kaye B. Tularemia and deer flies in the environs of Utah Lake, Utah. 25:13-29.
Cox, Mike K. and William L. Franklin. Terrestrial vertebrates of Scotts Bluff National Monument, Nebraska. 49:597-613.
Craig, T. H. *See* Gleason, R. L. 39:274-276.
Cramer, Kenneth L. and Joseph A. Chapman. Reproduction of three species of pocket mice (*Perognathus*) in the Bonneville Basin, Utah. 50:361-365.
______, A. Lee Foote, and Joseph A. Chapman. Small mammal records from Dolphin Island, the Great Salt Lake, and other localities in the Bonneville Basin, Utah. 50:283-285.
Crawford, John A., Walt Van Dyke, S. Mark Meyers, and Thomas F. Haensly. Fall diet of Blue Grouse in Oregon. 46:123-127.
______, Walter Van Dyke, Victor Coggins, and Martin St. Louis. Hatching chronology of Blue Grouse in northeastern Oregon. 46:745-748.
______. *See* Lutz, R. Scott. 49:252-258.
Creasy, James. *See* Finley, Robert B. 42:360.
Crellin, John R. Evaluation of a program to control hydatid disease in central Utah. 43:65-72.
Croft, B. A. Prey stage distribution, a factor affecting the numerical response of *Typhlodromus occidentalis* to *Tetranychus mcdanieli* and *Tetranychus pacificus*. 32:61-75.
______ and C. D. Jorgensen. *Typhlodromus mcgregori* Chant (Acarina: Phytoseiidae) and its control of phytophagous mites in Utah and southern California apple orchards. 37:366-374.
Cross, Jeffrey N. Contributions to the biology of the woundfin, *Plagopterus argentissimus* (Pisces: Cyprinidae), an endangered species. 38:463-468.
Cross, Stephen P. *See* McMahon, Ellen E. 41:270.
Cuk, Luka. *See* Seiler, Gerald J. 41:393-394.
Cully, Anne C. and Jack F. Cully, Jr. Spatial and temporal variability in perennial and annual vegetation at Chaco Canyon, New Mexico. 49:113-122.
Cully, Jack F., Jr. *See* Cully, Anne C. 49:113-122.
Cushing, Bruce S. and Anne Matherne. Stinger utilization and predation in the scorpion *Paruroctonus boreus*. 40:193-195.
Cushing, C. E. and R. T. Rader. A note on the food of *Callibaetis* (Ephemeroptera: Baetidae). 41:431-432.
______ and S. R. Rushforth. Diatoms of the Middle Fork of the Salmon River drainage, with notes on their relative abundance and distribution. 44:421-427.
______. *See* Barnes, James R. 46:204-207.

D

Daley, D. M. *See* Wallace, Richard L. 44:324-326.
Dalton, Larry B. *See* Greenwood, Charles L. 44:499-504.
Daniel, Joseph C., Jr. A note on the Common Loon in southern Colorado. 13:74.
______ and R. Leonard Blain. Background radiation and endemic faunal range in the San Luis Valley of southern Colorado. 19:37-42.
Dasmann, Marlene M. and Hobart M. Smith. A new sceloporine lizard form Oaxaca, Mexico. 34:231-237.
Davis, Donald W. *See* Titayavan, Manas 48:388-393.
Davis, James N. and Bruce L. Welch. Winter preference, nutritive value, and other range use characteristics of *Kochia prostrata* (L.) Schrad. 45:778-783.
______. *See* Skousen, J. 46:508-512.
______. *See* Stevens, Richard 41:274-277.
______. *See* Welch, Bruce L. 44:296-298.
Davis, Russell and David E. Brown. Role of post-Pleistocene dispersal on determining the modern distribution of Abert's squirrel. 49:425-434.
______ and Ronnie Sidner. Locality, habitat, and elevation records for the desert shrew, *Notiosorex crawfordi*. 49:140-141.
Davis, Tim D., N. Sankhla, W. R. Andersen, D. J. Weber, and B. N. Smith. High rates of photosynthesis in the desert shrub *Chrysothamnus nauseosus* ssp. *albicaulis*. 45:520-526.
Deacon, James E., Paul B. Schumann, and Edward L. Stuenkel. Thermal tolerances and preferences of fishes of the Virgin River system (Utah, Arizona, Nevada). 47:538-546.
______. *See* Baugh, Thomas M. 43:592-596; 46:441-444.
______. *See* Courtenay, Walter R. 42:361-366.

______. *See* Courtenay, Walter R., Jr. 47:523-526.
______. *See* Greger, Paul 42:549-552.
______. *See* Heckmann, Richard A. 46:662-676.
______. *See* Williams, Jack E. 46:220-223.
Decker, Lynn M. Coexistence of two species of sucker, *Catostomus*, in Sagehen Creek, California, and notes on their status in the western Lahontan Basin. 49:540-551.
Deisch, Michele S., Daniel W. Uresk, and Raymond L. Linder. Effects of prairie dog rodenticides on deer mice in western South Dakota. 50:347-353.
DeMarais, Bruce D. *See* Marsh, Paul C. 49:387-389.
Dempster, Lauramay T. and Friedrich Ehrendorfer. A new name for *Galium scabriusculum* (Rubiaceae) of Utah. 37:510.
Despain, Del W. and Grant A. Harris. Kramer Palouse natural area. 43:421-424.
Despain, William J. *See* Beck, D Elden 27:67-78.
Deutschman, Mark Robert. Grass spider microhabitat use in Organ Pipe Cactus National Monument, Arizona. 45:546-547.
Devine, Michael G. and Dennis K. Shiozawa. Littoral heterogeneity and diel behavior of white bass (*Morone chrysops*) and carp (*Cyprinus carpio*) in Utah Lake, Utah. 44:509-515.
Dewey, Douglas R. *See* Barkworth, Mary E. 43:561-572.
Dickinson, J. C. Notice of a new report entitled "Systematics collections: a national plan." 32:238.
Diem, Kenneth L. *See* Findholt, Scott L. 48:285-289.
Diller, Lowell V. and Richard L. Wallace. Additional distribution records and abundance of three species of snakes in southwestern Idaho. 41:154-157.
Dixon, James R. *See* Medica, Philip A. 35:317-318.
______. *See* Tanner, Wilmer W. 32:16-24.
Dixon, Verl G. Vasco M. Tanner--a participating citizen. 30:196.
Dobkin, David S. *See* Holmes, Jennifer A. 45:483-484.
Dobson, Martin L., Clyde L. Pritchett, and Jack W. Sites, Jr. Genetic variation and population structure in the cliff chipmunk, *Eutamias dorsalis*, in the Great Basin of western Utah. 47:551-561.
Doescher, Paul S., Richard F. Miller, Jianguo Wang, and Jeff Rose. Effects of nitrogen availability on growth and photosynthesis of *Artemisia tridentata* ssp. *wyomingensis*. 50:9-19.
Dole, Jim W. *See* Durant, Pedro 48:19-24.
Donahoo, Michael J. *See* Winger, Parley V. 32:211-219.
Dorn, Robert D. A new species of *Thelesperma* (Asteraceae) from Wyoming. 43:749-750.
______. *See* Lichvar, Robert W. 42:413-414; 43:739-740.
Douglas, Michael E. *See* Marsh, Paul C. 49:387-389.
Drake, Carl J. New African and Asian *Tingidae* (Hemiptera). 16:18-22.
______. New lacebugs from the eastern hemisphere. 23:149-158.
______. New neogaean Tingidae (Hemiptera). 13:13-16.
______. New Neotropical water-striders (Hemiptera-Veliidae). 11:37-42.
______. Synonymic data and descriptions of new genera and species of Tingidae (Hemiptera). 13:91-99.
______. Synonymical data: descriptions of new Hydrometridae (Hemiptera). 14:61-66.
______. Tingidae: descriptions and synonymic data (Hemiptera). 14:1-10.
______. Water-striders from Territorio Amazonas of Venezuela (Hemiptera; Hydrometridae, Veliidae). 12:47-54.
______ and Harold C. Chapman. Distributional data and description of a new hebrid (Hemiptera). 13:9-11.
______ and Richard C. Froeschner. A new myrmecophilous lacebug from Panama (Hemiptera: Tingidae). 22:8-11.
______ and Bob G. Hill. Some Ethiopian lacebugs (Hemiptera: Tingidae). 24:83-92.
______ and F. C. Hottes. Genus *Trepobates* Herrich-Schaeffer (Hemiptera; Gerridae). 12:35-38.
______ and F. C. Hottes. Saldidae of the Americas (Hemiptera). 10:51-61.
______ and F. C. Hottes. Stridulatory organs in Saldidae (Hemiptera). 11:43-46.
______ and David R. Lauck. Descriptions, synonymy, and check-list of American Hydrometridae (Hemiptera: Heteroptera). 19:43-52.
______ and David Livingstone. Two new species of lacebugs from India (Hemiptera: Tingidae). 24:27-30.
______ and M. Mohanasundarum. New Tingidae from South India (Hemiptera). 21:108-113.
______ and Florence A. Ruhoff. A necessary correction. 20:80.
______ and Florence A. Ruhoff. Tingidae: new genera, species, homonyms, and synonyms (Hemiptera). 20:29-38.
Drewes, Henry G. *See* Modde, Timothy 46:39-45.
Dudley, T. R. *Alyssum turgidum*: a new species from Iran. 24:7-12.
Duff, Donald A. *See* Hickman, Terry J. 38:193-202.
Duke, Kenneth L. A preliminary histological study of the ovary of the kangaroo rat *Dipodomys ordii columbianus*. 1:63-73.
______. Vasco M. Tanner--an inspiring teacher. 30:209-210.
Duncan, Russell B. and Ronnie Sidner. Bats in Spotted Owl pellets in southern Arizona. 50:197-200.
Dundee, Harold A. *See* Bragg, Arthur N. 9:55-57.
Dunn, Peter O. and Ronald A. Ryder. Notes on the birds of Cold Spring Mountain, northwestern Colorado. 46:651-655.
Durant, Pedro, Jim W. Dole, and George F. Fisler. Agonistic behavior of the California ground squirrel, *Spermophilus beecheyi*, at an artificial food source. 48:19-24.
Duvall, David. *See* Anderson, Stanley H. 47:512-521.

E

Eads, Richard B. Two new species of fleas of the genus *Meringis* (Siphonaptera: Hystrichopsyllidae). 38:447-455.

______ and E. G. Campos. Deer mouse, *Peromyscus maniculatus*, and associated rodent fleas (Siphonaptera) in the arctic-alpine life zone of Rocky Mountain National Park, Colorado. 43:168-174.

______ and E. G. Campos. Description of a new *Phalacropsylla* and notes on *P. allos* (Siphonaptera: Hystrichopsyllidae). 42:241-245.

______ and G. O. Maupin. Description of the female of *Phalacropsylla hamata* (Siphonaptera: Hystrichopsyllidae). 42:96-99.

Eames, Michael. *See* Erman, Don C. 37:57-66.

Eckert, Richard E., Jr. *See* Tueller, Paul T. 47:117-131.

Eddleman, Lee E. *See* Miller, Richard F. 47:349-354.

Edminster, Carleton B. *See* Mathiasen, Robert L. 46:277-280; 46:685-689; 47:467-472; 50:67-71; 50:173-179.

Egoscue, Harold J. Additional records of the dark kangaroo mouse (*Microdipodops megacephalus nasutus*), with a new maximum altitude. 41:333-334.

______. Flea exchange between deer mice and some associated small mammals in western Utah. 36:475-480.

______. New and additional host-flea associations and distributional records of fleas from Utah. 26:71-75.

______. Noteworthy flea records from Utah, Nevada, and Oregon. 48:530-532.

______. The sagebrush vole flea, *Megabothris clantoni princei*, in western Utah, with comments on the distribution of *Megabothris* in the Bonneville Basin. 37:75-76.

______. Shrew and heteromyid records from the Great Basin of Oregon and Utah. 48:267-268.

______. Woodrat nest flea *Anomiopsyllus amphibolus* in southeastern Oregon. 40:361.

______ and Elizabeth S. Frank. Burrowing and denning habits of a captive colony of the Utah prairie dog. 44:495-498.

______. *See* Lowry, Elbert J. 28:47.

Ehleringer, James and Donna House. Orientation and slope preference in barrel cactus (*Ferocactus acanthodes*) at its northern distribution limit. 44:133-139.

Ehrendorfer, Friedrich. *See* Dempster, Lauramay T. 37:510.

Ekins, Laura and Samuel R. Rushforth. Diatom flora of Cowboy Hot Spring, Mono County, California. 46:612-624.

Elder, John A. and Arden R. Gaufin. Notes on the occurrence and distribution of *Pteronarcys californica* Newport (Plecoptera) within streams. 33:218-220.

Elias, Scott A. Colorado ground beetles (Coleoptera: Carabidae) from the Rotger Collection, University of Colorado Museum. 47:631-637.

Elliott, Charles L. and Jerran T. Flinders. Cranial measurements of the Columbian ground squirrel (*Spermophilus columbianus columbianus*), with special reference to subspecies taxonomy and juvenile skull development. 44:505-508.

______ and Jerran T. Flinders. Plant nutrient levels on two summer ranges in the River of No Return Wilderness Area, Idaho. 44:621-626.

______ and Jerran T. Flinders. Postemergence development and interyear residence of juvenile Columbian ground squirrels in the Idaho primitive area. 40:362-364.

______ and Jerran T. Flinders. Seasonal activity pattern of Columbian ground squirrels in the Idaho primitive area. 40:175-177.

______ and Richard Guetig. Summer food habits of coyotes in Idaho's River of No Return Wilderness Area. 50:63-65.

Elliott, Nancy B. and Frank E. Kurczewski. Nesting and predatory behavior of some *Tachysphex* from the western United States (Hymenoptera: Sphecidae). 45:293-298.

Elliott-Fisk, Deborah L., Betty S. Adkins, and Jeanine L. Spaulding. A reevaluation of the postglacial vegetation of the Laramie Basin, Wyoming-Colorado. 43:377-384.

Ellis, David E. *See* Weston, J. Bradford 28:111.

Ellis, David H., Dwight G. Smith, and Joseph R. Murphy. Studies on raptor mortality in western Utah. 29:165-167.

Ellis, Kevin L. and Jimmie R. Parrish. A case of leucism in the Western Bluebird (*Sialia mexicana*). 48:75-77.

______, Jimmie R. Parrish, and Gary H. Richins. Habitat use by breeding male Sage Grouse: a management approach. 49:404-407.

Emison, William B. and Clayton M. White. Foods and weights of the Rock Ptarmigan on Amchitka, Aleutian Islands, Alaska. 48:533-540.

Emmerson, F. H. *See* Anderson, B. B. 30:107.

Emmerson, Frederick H. Western diamondback rattlesnake in southern Nevada: a correction and comments. 42:350.

Engelking, L. D. *See* Bourgeron, P. S. 50:209-242.

England, John Larry. A new species of *Penstemon* (Scrophulariaceae) from the Uinta Basin of Utah and Colorado. 42:367-368.

Engstrom, Mark D. and Eugene D. Fleharty. Range extension of *Onychomys torridus longicaudus* (Rodentia: Cricetidae) in northwestern Nevada. 38:180.

Erman, Don C. Peat depth of Sierra Nevada fens and profile changes from 1958 to 1972 in Mason Fen. 36:101-107.

______, Kenneth B. Roby, and Michael Eames.

Hydrological features of a California coastal fen. 37:57-66.

Erman, Nancy A. Species composition, emergence, and habitat preferences of Trichoptera of the Sagehen Creek basin, California, USA. 49:186-197.

Ertter, Barbara J. *See* Reveal, James L. 36:272-280.

Evans, Howard E. Further studies on the wasps of Jackson Hole, Wyoming (Hymenoptera, Aculeata). 33:147-155.

______. The nest and larva of *Diploplectron brunneipes* (Cresson) (Hymenoptera: Sphecidae). 35:123-125.

______. Nests and prey of two species of *Philanthus* in Jackson Hole, Wyoming (Hymenoptera, Sphecidae). 26:35-40.

______. New distribution records of spider wasps (Hymenoptera, Pompilidae) from the Rocky Mountain states. 50:193-195.

______. Notes on the nesting behavior of *Steniolia elegans* (Hymenoptera: Sphecidae). 33:29-30.

______. Observations on natural enemies of western spruce budworm (*Choristoneura occidentalis* Freeman)(Lepidoptera, Tortricidae) in the Rocky Mountain area. 47:319-321.

______ and William L. Rubink. Observations on the prey and nests of seven species of *Cerceris* (Hymenoptera: Sphecidae). 38:59-63.

Evans, Mary Alice. Checklist of the Odonata of Colorado. 48:96-101.

Evans, R. Scott. *See* Palmieri, James R. 36:86-96.

Evans, Raymond A. *See* Young, James A. 46:1-21.

Evenson, William E., Jack D. Brotherson, and Richard B. Wilcox. Relationship between environmental and vegetational parameters for understory and open-area communities. 40:167-174.

______. *See* Brotherson, Jack D. 40:229-253; 41:298-309; 45:1-13.

______. *See* Grimes, Judith A. 44:36-48.

Everett, Richard L. Understory seed rain in harvested pinyon-juniper woodlands. 46:706-710.

______ and Susan Koniak. Understory vegetation in fully stocked pinyon-juniper stands. 41:467-475.

______ and Steven H. Sharrow. Understory response to tree harvesting of singleleaf pinyon and Utah juniper. 45:105-112.

______. *See* Wilt, F. Martin 48:228-231.

Evert, Erwin F. and Ronald L. Hartman. Additions to the vascular flora of Wyoming. 44:482-483.

______. *See* Lichvar, Robert W. 43:739-740.

F

Fairchild, John. *See* Brotherson, J. D. 38:19-30.

______. *See* Brotherson, Jack D. 45:1-13.

Fall, Michael W. *See* LaVoie, G. Keith 31:181.

Fanghella, Charles, David F. Avery, and Wilmer W. Tanner. *Urosaurus* and its phylogenetic relationship to *Uta* as determined by osteology and myology (Reptilia: Iguanidae). 35:245-268.

Farentinos, R. C. *See* Pederson, Jordan C. 47:252-258.

Farnsworth, R. B., E. M. Romney, and A. Wallace. Implications of symbiotic nitrogen fixation by desert plants. 36:65-80.

Farrar, P. A. *See* Schmid, J. M. 41:465-466.

Fautin, Reed W. The establishment and maintenance of territories by the Yellow-headed Blackbird in Utah. 1:75-91.

Fawcett, James D. and Hobart M. Smith. The lizard *Leiolopisma smithi* Cochran, a junior secondary homonym of *Mocoa smithi* Gray. 31:135-137.

______ and Hobart M. Smith. Nomenclatural problems concerning the generic and familial names for the New Zealand and American ribbed frogs. 31:261-264.

Fay, Harlan. *See* Li, C. Y. 46:646-650.

Feddema, C. *See* Wilken, D. 38:208-210.

Feduccia, Alan and Charles G. Oviatt. Trumpeter Swan (*Cygnus buccinator*) from the Pleistocene of Utah. 46:547-548.

Feldhamer, George A. Vegetative and edaphic factors affecting abundance and distribution of small mammals in southeast Oregon. 39:207-218.

Fend, Steven V. *See* Leland, Harry V. 46:595-611.

Ferguson, Denzel E., K. Ellsworth Payne, and Robert M. Storm. Notes on the herpetology of Baker County, Oregon. 18:63-65.

Ferrington, Leonard C., Jr. *See* Swegman, Bernard G. 40:287-291.

Feuer, Robert C. and Hobart M. Smith. The contributions of the 1822 works of Jarocki and Fleming to herpetological nomenclature. 32:55-60.

Ffolliott, Peter F. *See* Clary, Warren P. 44:627-634.

Fielding, Max J. Three new predacious nematodes. 10:45-50.

Findholt, Scott L. First nest records for the Plain Titmouse and Blue-gray Gnatcatcher in Wyoming. 43:747-748.

______. Status and distribution of California Gull nesting colonies in Wyoming. 46:128-133.

______ and Kevin L. Berner. Current status and distribution of the Ciconiiforms nesting in Wyoming. 48:290-297.

______ and Kenneth L. Diem. Status and distribution of American White Pelican nesting colonies in Wyoming: an update. 48:285-289.

Finley, Robert B., Jr. and James Creasy. First specimen of the spotted bat (*Euderma maculatum*) from Colorado. 42:360.

______, William Caire, and Dallas E. Wilhelm. Bats of the Colorado oil shale region. 43:554-560.

Fischer, David L. First records of the Glaucous-winged Gull in Utah. 48:298-300.

Fisher, D. Lowell. *See* Tanner, Wilmer W. 31:213-222.

Fisler, George F. *See* Durant, Pedro 48:19-24.

Flake, Lester D. and Clive D. Jorgensen. Invasion of a "trapped-out" southern Nevada habitat by *Perognathus longimembris*. 29:143-149.

Flath, Dennis L. *See* Burns, James A. 49:517-524.

______. *See* Shryer, Jeff 40:115.

Fleharty, Eugene D. *See* Engstrom, Mark D. 38:180.

Flinders, Jerran T. *See* Elliott, Charles L. 40:175-177; 40:362-364; 44:505-508; 44:621-626.

______. *See* Green, Jeffrey S. 39:88; 41:158-160; 41:251-254.

______. *See* Slaugh, Bartel T. 49:632-636; 50:379-380.

______. *See* Steigers, William D. 42:567-571.

______. *See* Zou, Jiping. 49:435-448.

Foote, A. Lee. Response of nesting waterfowl to flooding in Great Salt Lake wetlands. 49:614-617.

______. *See* Cramer, Kenneth L. 50:283-285.

Forcella, F. *See* Weaver, T. 37:395-401.

Forsythe, Dennis M. Observations on the nesting biology of the Long-billed Curlew. 32:88-90.

Foster, Susan Q. *See* Bushnell, John H. 47:500-511.

Fouquette, M. J., Jr. Remarks on the type specimen of *Bufo alvarius* Girard. 28:70-72.

Fox, J. Carl, Ferron L. Andersen, and Keith H. Hoopes. A survey of the helminth parasites of cattle and sheep in Utah Valley. 30:131-145.

______. *See* Andersen, Ferron L. 29:35-41.

Frank, Elizabeth S. *See* Egoscue, Harold J. 44:495-498.

Franklin, William L. *See* Cox, Mike K. 49:597-613.

Fredericks, S. E. and M. J. Jenkins. Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins, Coleoptera: Scolytidae) brood production on Douglas-fir defoliated by western spruce budworm (*Choristoneura occidentalis* Freeman, Lepidoptera: Tortricidae) in Logan Canyon, Utah. 48:348-351.

Freeman, C. Edward. *See* Reid, William H. 48:489-494.

Freeman, D. Carl. *See* McArthur, E. Durant 46:157-160.

Freeman, Patricia W. *See* Lemen, Cliff A. 47:1-6.

French, Thomas W. *See* Brown, Barbara A. 46:421-426.

Fresquez, P. R. Fungi associated with soils collected beneath and between pinyon and juniper canopies in New Mexico. 50:167-172.

Frischknecht, Neil C. *See* Buchanan, Bruce A. 38:90-96.

Froeschner, Richard C. Lace bugs collected during the Bredin-Archbold-Smithsonian biological survey of Dominica, B. W. I. (Hemiptera: Tingidae). 28:161-171.

______. New records of lace bugs from Nevada (Hemiptera: Tingidae). 31:160.

______. Zoogeographic and systematic notes on the lace bug tribe Litadeini, with the description of the new genus *Stragulotingis* (Hemiptera: Tingidae). 29:129-132.

______. *See* Drake, Carl J. 22:8-11.

Frost, Herbert H. *See* Smith, Dwight G. 32:229-234.

______. *See* White, Clayton M. 43:717-727.

Furniss, Malcolm M. and James B. Johnson. List of Idaho Scolytidae (Coleoptera) and notes on new records. 47:375-382.

______ and Gordon A. Van Epps. Bionomics and control of the walnut spanworm, *Phigalia plumogeraria* (Hulst), on bitterbrush in Utah. 41:290-297.

______. *See* Bales, Frances M. 44:338-348.

______. *See* Gast, Sandra J. 49:381-386.

G

Gagne, Raymond J. A new species of *Rhopalomyia* (Diptera: Cecidomyiidae) from *Artemisia ludoviciana* Nuttall (Compositae) in Utah. 37:426-428.

Gakahu, Christopher G. *See* Cox, George W. 47:609-619.

Galat, David L. and Nancy Vucinich. Food of larval tui chubs, *Gila bicolor*, in Pyramid Lake, Nevada. 43:175-178.

Galatowitsch, S. M. Using the original land survey notes to reconstruct presettlement landscapes in the American West. 50:181-191.

Gallup, John S. *See* Morton, Martin L. 35:427-433.

Galton, Peter M. and James A. Jensen. Small bones of the hypsilophodontid dinosaur *Dryosaurus altus* from the upper Jurassic of Colorado. 33:129-132.

Garcia, James R. *See* Jorgensen, Clive D. 40:282-286.

Gast, Sandra J., Malcolm M. Furniss, James B. Johnson, and Michael A. Ivie. List of Montana Scolytidae (Coleoptera) and notes on new records. 49:381-386.

Gates, G. E. On the earthworm fauna of the Great American Desert and adjacent areas. 27:142-176.

______. On two little-known species of the earthworm genus *Diplocardia*. 27:1-10.

Gaufin, Arden R., Robert Clubb, and Robert Newell. Studies on the tolerance of aquatic insects to low oxygen concentrations. 34:45-59.

______. *See* Branham, Joseph M. 35:51-61.

______. *See* Cather, Mary R. 35:39-48; 35:49-50.

______. *See* Elder, John A. 33:218-220.

______. *See* Stark, Bill P. 34:83-93; 35:97-99.

Gennaro, A. L. *See* Best, Troy L. 45:527-534.

Genter, David L. Wintering bats of the upper Snake River plain: occurrence in lava-tube caves. 46:241-244.

Germano, David J. and C. Roger Hungerford. Reptile population changes with manipulation of Sonoran Desert shrub. 41:129-138.

______ and David N. Lawhead. Species diversity and habitat complexity: Does vegetation organize vertebrate communities in the Great Basin? 46:711-720.

Gersberg, R. M. *See* Axler, R. P. 38:187-192.

Gessaman, James A. Body fat, body water, and total caloric value of Uinta ground squirrels. 44:176-177.

______ and Andrew G. Goliszek. Marmot scats supplement hay pile vegetation as food energy for pikas. 49:466-468.

Ghiselin, Jon. Individual rodent movements in upper Sonoran Desert of central Nevada. 29:109-110.

______. *See* Behle, William H. 18:1-22.

Gilbertson, R. L. and J. P. Lindsey. Basidiomycetes that decay junipers in Arizona. 35:288-304.

______ and J. P. Lindsey. Basidiomycetes that decay junipers in Arizona. II. 38:42-48.

Gilland, James K. *See* Rigby, J. Keith 37:475-480

Gillman, Leah A. *See* Taylor, Frances R. 49:491-495.

Gist, Clayton S. Problems of sampling desert arthropods before and after a thermonuclear cratering test. 27:26-35.

Gleason, R. L. and T. H. Craig. Food habits of Burrowing Owls in southeastern Idaho. 39:274-276.

Gleason, Richard S. and Donald R. Johnson. Factors influencing nesting success of Burrowing Owls in southeastern Idaho. 45:81-84.

Glenn, James L., Richard C. Straight, and Jack W. Sites, Jr. A plasma protein marker for population genetic studies of the desert tortoise (*Xerobates agassizi*). 50:1-8.

Goates, Morris A. *See* Allred, Dorald M. 24:71-73.

Goff, M. L. and J. M. Brennan. A new monotypic genus of chiggers and four new species of *Quadraseta* from Venezuela (Acari: Trombiculidae). 37:501-509.

Goldman, Charles R. *See* Mahood, Albert D. 44:83-98.

Golightly, Richard T., Jr. *See* Green, Jeffrey S. 45:567-570.

Goliszek, Andrew G. *See* Gessaman, James A. 49:466-468.

Goodrich, John M. and San J. Stiver. Co-occupancy of a den by a pair of Great Basin black bears. 49:390-391.

Goodrich, Sherel. Checklist of vascular plants of the Canyon and Church mountains. 44:277-295.

______. Utah flora: Apiaceae (Umbelliferae). 46:66-106.

______. Utah flora: Juncaceae. 46:366-377.

______. Utah flora: Salicaceae. 43:531-550.

______. Utah flora: Saxifragaceae. 45:155-172.

______ and Stanley L. Welsh. New variety of *Stephanomeria tenuifolia* (Compositae) from Utah. 43:375.

______, E. Durant McArthur, and Alma H. Winward. A new combination and a new variety in *Artemisia tridentata*. 45:99-104.

______. *See* Atwood, Duane 44:263-264.

______. *See* Welsh, S. L. 41:1-108.

______. *See* Welsh, Stanley L. 40:78-88; 45:34-36.

Gordon, Christine C. Winter food habits of the pine marten in Colorado. 46:166-168.

Gould, William. Aspects of the biology of the flathead chub (*Hybopsis gracilis*) in Montana. 45:332-336.

Grabowski, William B. A new species of oribatid mite (Cryptostigmata: Oribatellidae). 30:5-8.

Grant, C. Val. Wildlife distribution and abundance on the Utah Oil Shale Tracts, 1975-1984. 46:469-507.

Graybosch, Robert A. and Hayle Buchanan. Vegetative types and endemic plants of the Bryce Canyon Breaks. 43:701-712.

______. *See* Buchanan, Hayle 41:109-120.

______. *See* Clark, Stephen L. 41:269.

Grayson, Donald K. and Stephanie D. Livingston. High-elevation records for *Neotoma cinerea* in the White Mountains, California. 49:392-395.

Grebence, Brandon L. and Clayton M. White. Physiographic characteristics of Peregrine Falcon nesting habitat along the Colorado River system in Utah. 49:408-418.

Green, Jeffrey S. and Jerran T. Flinders. Alarm call of the pygmy rabbit (*Brachylagus idahoensis*). 41:158-160.

______ and Jerran T. Flinders. Diets of sympatric red foxes and coyotes in southeastern Idaho. 41:251-254.

______ and Jerran T. Flinders. Homing by a pygmy rabbit. 39:88.

______, Richard T. Golightly, Jr., Susan Lyndaker Lindsey, and Brad R. LeaMaster. Use of radio transmitter implants in wild canids. 45:567-570.

Greenwood, Charles L. and Larry B. Dalton. Mule deer passage beneath an overland coal conveyer. 44:499-504.

Greger, Paul and James E. Deacon. Observations on woundfin spawning and growth in an outdoor experimental stream. 42:549-552.

______. *See* Heckmann, Richard A. 46:662-676.

Gregg, Robert E. A new species of *Stenamma* (Hymenoptera: Formicidae) from Utah. 32:35-39.

Griffith, J. S., Jr. *See* Wallace, Richard L. 44:324-326.

Grimes, Judith A., Samuel R. Rushforth, Jack D. Brotherson, and William E. Evenson. Diatoms in recent bottom sediments and trophic status of eight lakes and reservoirs in northeastern Utah. 44:36-48.

______, Larry L. St. Clair, and Samuel R. Rushforth. A comparison of epiphytic diatom assemblages on living and dead stems of the common grass *Phragmites australis*. 40:223-228.

______. *See* Rushforth, Samuel R. 40:98-100.

Grogan, William L., Jr. and Lloyd C. Pack, Jr. Notes on reproduction in *Lampropeltis triangulum* and *Coluber constrictor* in Utah. 33:202.

______ and Wilmer W. Tanner. Range extension of the long-nosed snake, *Rhinocheilus l. lecontei*, into east-central Utah. 34:238-240.

______ and Willis W. Wirth. A revision of the Nearctic species of *Clinohelea* Kieffer (Diptera: Ceratopogonidae). 35:275-287.

Groves, Craig R. and Barry L. Keller. Hip glands in a natural population of montane voles (*Microtus montanus*). 44:468-470.

______ and Barry L. Keller. Movements by small mammals on a radioactive waste disposal area in southeastern Idaho. 46:404-410.

______. *See* Campbell, Thomas M., III 42:100.

Grundmann, Albert W. *See* Bienek, Gerhard K. 31:190-192.

Guenther, Herbert R. *See* Judd, B. Ira 31:153-159.

Guetig, Richard. *See* Elliott, Charles L. 50:63-65.

Guibé, Jean. *See* Smith, Hobart M. 35:109-112.

Guimarães, Lindolpho R. Supplementary note on Venezuelan bat flies (Diptera: Nycteribiidae). 37:221-224.

Gustafson, Eric S. *See* Minckley, W. L. 42:553-561.

Gut, Larry J., Robert A. Schlising, and Carol E. Stopher. Nectar-sugar concentrations and flower visitors in the western Great Basin. 37:523-529.

Gutzwiller, Kevin J. and Stanley H. Anderson. Trees used simultaneously and sequentially by breeding cavity-nesting birds. 46:358-360.

Guyer, Craig and Allan D. Linder. Thermal ecology and activity patterns of the short-horned lizard (*Phrynosoma douglassi*) and the sagebrush lizard (*Sceloporus graciosus*) in southeastern Idaho. 45:607-614.

H

Haensly, Thomas F. *See* Crawford, John A. 46:123-127.

Haferkamp, Marshall R. *See* Romo, James T. 47:110-116.

Halford, Douglas K. and Jere B. Millard. Vertebrate fauna of a radioactive leaching pond complex in southeastern Idaho. 38:64-70.

______, W. John Arthur III, and A. William Alldredge. Observations of captive Rocky Mountain mule deer behavior. 47:105-109.

______. *See* Reynolds, Timothy D. 46:513-527.

Hall, Deborah A. and Penny S. Amy. Microbiology and water chemistry of two natural springs impacted by grazing in south central Nevada. 50:289-294.

Hall, E. Raymond and C. Lynn Hayward. Three new mammals (*Microtus* and *Ochotona*) from Utah. 2:105-108.

Hall, William P. *See* Smith, Hobart M. 34:97-104.

Hallsten, Gregory P. and David W. Roberts. Additions to the vascular flora of Bryce Canyon National Park, Utah. 48:352.

Hamrick, J. L. *See* Hiebert, R. D. 44:487-494.

Hancock, Denis C., Jr., and Donald J. Nash. Dorsal hair length and coat color in Abert's squirrel (*Sciurus aberti*). 42:597-598.

Handegarde, Royal. *See* Judd, B. Ira 31:153-159.

Hanks, L. M. *See* Rust, R. W. 43:403-408.

Hansen, Afton M. and Wilmer W. Tanner. A comparative osteological study of certain species belonging to the genus *Bolitoglossa* (Amphibia). 18:85-100.

Hansen, Charles G. Ectoparasites of mammals from Oregon. 24:75-81.

______. *See* Bradley, W. Glen 28:199.

Hansen, D. J. and D. J. Weber. Environmental factors in relation to the salt content of *Salicornia pacifica* var. *utahensis*. 35:86-96.

Hansen, George H. Vasco M. Tanner--colleague and friend. 30:218.

Hansen, James D. Comparison of insects from burned and unburned areas after a range fire. 46:721-727.

______. Field observations of *Irbisia pacifica* (Hemiptera: Miridae): feeding behavior and effects on host plant growth. 48:68-74.

______. Trapping methods for rangeland insects in burned and unburned sites: a comparison. 48:383-387.

Hansen, R. M. *See* Cincotta, R. P. 47:339-343.

Hansen, Richard M. *See* MacCracken, James G. 42:45-49; 43:660-668; 45:287-290; 46:274-276.

Harding, William J. The algae of Utah Lake, Part II. 31:125-134.

______. A preliminary report on the algal species presently found in Utah Lake. 30:99-105.

Harmon, W. *See* Wilken, D. 38:208-210.

Harmston, Fred C. An annotated list of mosquito records from Colorado. 9:65-75.

______. Dipterous predators of the mosquito in Utah and Wyoming. 9:21-23.

______. New species of Dolichopodidae from California and Utah (Diptera). 11:11-17.

______. *See* Knowlton, George F. 3:22.

Harniss, R. O. *See* McDonough, W. T. 35:325-326.

Harper, K. T. *See* Buchanan, Bruce A. 38:90-96.

______. *See* Kunzler, L. M. 40:127-130; 41:147-153.

______. *See* Pederson, Jordan C. 39:122-128.

Harper, Kimball T. *See* Collins, Patrick D. 43:385-393.

______. *See* Marble, James R. 49:104-107.

Harrington, H. *See* Wilken, D. 38:208-210.

Harris, Don R. *See* Tanner, Vasco M. 29:150-164; 29:183-205.

Harris, Grant A. *See* Despain, Del W. 43:421-424.

Harris, Herbert S., Jr. *See* Tanner, Wilmer W. 32:16-24.

Harris, James G. A vascular flora of the San Rafael Swell, Utah. 43:79-87.

Harrison, Bertrand F. Tribute to Vasco Tanner. 30:205-206.

Hart, E. B. Food preferences of the cliff chipmunk, *Eutamias dorsalis*, in northern Utah. 31:182-188.

Hart, E. Blake. Intercanine crown distances in red foxes and badgers. 42:601-602.

______. The raccoon, *Procyon lotor*, in Wyoming. 42:599-600.

______ and Michael Trumbo. Winter stomach contents of South Dakota badgers. 43:492-493.

Hartman, Emily L. and Mary Lou Rottman. Alpine vascular flora of the Ruby Range, West Elk Mountains, Colorado. 47:152-160.

______. *See* Rottman, Mary Lou 45:87-93.

Hartman, Ronald L. and Robert W. Lichvar. Additions to the vascular flora of Teton County, Wyoming. 40:408-413.

______. *See* Evert, Erwin F. 44:482-483.

Hassler, Thomas J. *See* Vigg, Steven 42:529-540.

Hatch, Stephan L. New grass distribution records for Arizona, New Mexico, and Texas. 40:221-222.

______. New grass distribution records for New Mexico

and the United States. 37:530-531.
______. A taxonomic evaluation of *Elymus simplex* (Poaceae). 36:239-241.
Hathaway, Ralph R. Sexual dimorphism in malpighian tubules of *Pteronarcys californica* Newport (Plecoptera). 35:449-451.
Haufler, Jonathan B. and Julius G. Nagy. Summer food habits of a small mammal community in the pinyon-juniper ecosystem. 44:145-150.
Haukos, D. A. and L. M. Smith. Lesser Prairie-Chicken nest site selection and vegetation characteristics in tebuthiuron-treated and untreated sand shinnery oak in Texas. 49:624-626.
Hauptman, Tedd N. *See* Clark, Tim W. 49:587-596.
Hawksworth, Frank G. and Robert L. Mathiasen. Hosts of juniper mistletoe at Walnut Canyon National Monument, Arizona. 38:89.
______. *See* Mathiasen, Robert L. 46:685-689; 50:67-71; 50:91-92; 50:173-179.
Hayward, B. J. *See* Severson, K. E. 48:554-557.
Hayward, C. Lynn. A bibliography of Utah mammalogy; including references to names and type localities (first supplement). 2:125-136.
______. Biotic communities of the southern Wasatch and Uinta mountains, Utah. 6:1-124.
______. John Hutchings and Robert G. Bee--pioneer Utah Valley naturalists. 3:86-90.
______. Notes on the distribution of nighthawks in Utah. 1:93-96.
______. Notes on the nesting habits of some mountain dwelling birds in Utah. 2:1-8.
______. Vasco M. Tanner. 30:181-189.
______ and Merlin L. Killpack. Distribution and variation of the Utah population of the Great Basin pocket mouse. 18:26-30.
______. *See* Hall, E. Raymond 2:105-108.
______. *See* Killpack, Merlin L. 18:23-25.
Heaton, Timothy H. Quaternary paleontology and paleoecology of Crystal Ball Cave, Millard County, Utah: with emphasis on mammals and description of a new species of fossil skunk. 45:337-390.
Heckmann, Richard. Eye fluke (*Diplostomum spathaceum*) of fishes from the upper Salmon River near Obsidian, Idaho. 43:675-683.
______ and T. Carroll. Host-parasite studies of *Trichophrya* infesting cutthroat trout (*Salmo clarki*) and longnose suckers (*Catostomus catostomus*) from Yellowstone Lake, Wyoming. 45:255-265.
______ and H. L. Ching. Parasites of the cutthroat trout, *Salmo clarki*, and longnose suckers, *Catostomus catostomus*, from Yellowstone Lake, Wyoming. 47:259-275.
______ and Bruce A. Coleman. Parasites of Indochinese refugees entering Utah County, Utah: a two-year survey. 41:201-206.
______ and Terry Otto. Occurrence of anisakid larvae (Nematoda: Ascardidia) in fishes from Alaska and Idaho. 45:427-431.
______ and James R. Palmieri. The eye fluke disease (Diplostomatosis) in fishes from Utah. 38:473-477.
______, James E. Deacon, and Paul D. Greger. Parasites of the woundfin minnow, *Plagopterus argentissimus*, and other endemic fishes from the Virgin River, Utah. 46:662-676.
______, Lauritz A. Jensen, Robert G. Warnock, and Bruce Coleman. Parasites of the bowhead whale, *Balaena mysticetus*. 47:355-372.
______, Allen K. Kimball, and Jeffery A. Short. Parasites of mottled sculpin, *Cottus bairdi* Girard, from five locations in Utah and Wasatch counties, Utah. 47:13-21.
______, Robert N. Winget, Rex C. Infanger, Roger W. Mickelsen, and John M. Hendersen. Warm water aquaculture using waste heat and water from zero discharge power plants in the Great Basin. 44:75-82.
______. *See* Brienholt, Craig 40:149-156.
______. *See* Henderson, J. M. 44:471-481.
______. *See* Mickelsen, Roger W. 39:231-240.
______. *See* Otto, Terry N. 44:125-132.
______. *See* Palmieri, James R. 36:86-96.
______. *See* Wadley, S. R. 42:67-72.
______. *See* Yi, Jea Kim 48:206-215.
Hegerhorst, D. F., R. B. Bhat, D. J. Weber, and E. D. McArthur. Seasonal changes of selected secondary plant products in *Chrysothamnus nauseosus* ssp. *turbinatus*. 48:1-8.
Heil, Ken and Stanley L. Welsh. New *Sclerocactus* (Cactaceae) from Nevada. 46:677-678.
______, J. Mark Porter, and Stanley L. Welsh. A new species of *Asclepias* (Asclepiadaceae) from northwestern New Mexico. 49:100-103.
Hellenthal, Ronald A. *See* Patton, James L. 44:431-440.
Helm, William T. *See* Sigler, William F. 43:1-29.
Hendersen, John M. *See* Heckmann, Richard A. 44:75-82.
Henderson, Douglass M. *See* Cholewa, Anita F. 44:140-144.
Henderson, J. M., R. A. Heckmann, and R. N. Winget. Multiple use systems for aquaculture. 44:471-481.
Henderson, Jan A. *See* Schimpf, David J. 40:1-26.
Henderson, W. W. Four devastating Melanopli found in Utah (Orthoptera - Cyrtacanthacrinae). 5:1-22.
______. The genus *Hesperotettix* in Utah (Orthoptera, Locustidae, Cyrtacanthacrinae). 3:9-21.
______. Some corrections in *Hesperotettix*. 6:126.
Henry, Stephen E., Martin G. Raphael, and Leonard F. Ruggiero. Food caching and handling by marten. 50:381-383.
Heringhi, H. L. *See* Nickerson, Max A. 26:136-140.
Herrin, C. Selby. *Dermacentor andersoni* in national forest recreation sites of Utah. 28:30-43.
______. Incidence of spotted fever in wood ticks of Utah recreational sites. 33:26-28.
______ and Vernon J. Tipton. A systematic revision of the genus *Laelaps* s. str. (Acari: Mesostigmata) of

the Ethiopian region. 36:113-205.
Hess, M. W. *See* Huang, J. 48:334-347.
______. *See* Khan, M. A. 47:91-95.
______. *See* Nambudiri, E. M. V. 41:161-166.
Hess, William J. and James L. Reveal. A revision of *Eriogonum* (Polygonaceae) subgenus *Pterogonum*. 36:281-333.
Hiatt, Robert W. A frequency distribution of Eastern and Western Kingbirds in Montana. 3:109-114.
Hickman, Gary L. Dead Great Blue Heron found at 11,000 foot Utah elevation. 32:112.
Hickman, Terry J. and Donald A. Duff. Current status of cutthroat trout subspecies in the western Bonneville Basin. 38:193-202.
Hiebert, R. D. and J. L. Hamrick. An ecological study of bristlecone pine (*Pinus longaeva*) in Utah and eastern Nevada.
44:487-494.
Higgins, Harold G. A new beetle mite from Utah (*Oribatei*: *Gymnodamaeidae*). 21:27-28.
______. A new species of *Eremaeus* from the western United States (Acarina: Oribatei, Eremaeidae). 22:89-92.
______. Two new mites from the United States (Acari: Oribatei, Microzetidae, and Oribatellidae). 25:55-58.
______ and Stanley B. Mulaik. A new *Caeculus* from Oregon (Acarina: Caeculidae). 17:27-29.
______ and Tyler A. Woolley. *Ametroproctus*: a new genus of charassobatid mites from the United States. (Acari: Cryptostigmata: Charassobatidae). 28:44-46.
______ and Tyler A. Woolley. A new mite of the genus *Eupterotegaeus* from Oregon (Cryptostigmata: Cepheidae). 28:179-182.
______ and Tyler A. Woolley. New mites from the Yampa Valley (Acarina: Cryptostigmata: Oribatulidae, Passalozetidae). 35:103-108.
______ and Tyler A. Woolley. A new species of *Liacarus* for a wood rat nest (Acarina: Cryptostigmata, Liacaridae). 29:140-142.
______ and Tyler A. Woolley. New species of oribatids from western Colorado (Acarina: Cryptostigmata, Suctobelbidae). 36:496-500.
______ and Tyler A. Woolley. A new species of *Passalozetes* from Utah with notes on the genus (Acarina: Oribatei). 22:93-100.
______ and Tyler A. Woolley. A new species of soil mite from western Colorado (Acari: Cryptostigmata, Pelopidae). 32:208-210.
______ and Tyler A. Woolley. Redescription of *Microzetes auxiliaris appalachicola* Jacot (Acari: Cryptostigmata, Microzetidae). 28:142-143.
______. *See* Woolley, Tyler A. 25:59-62; 28:144-146; 28:172-175; 28:176-178; 33:37-42.
Higgins, Larry C. Boraginaceae of the southwestern United States. 39:293-350.
______. New combinations and a new species of perennial *Cryptantha*. 29:28-30.
______. New species of perennial *Cryptantha* from Utah. 28:195-198.
______. Plants new to the Utah flora. 32:117-119.
______. A revision of the *Echidiocarya* section of *Plagiobothrys* (Boraginaceae). 34:161-166.
______. *See* Stewart, Kenneth W. 36:366-384.
______. *See* Thorne, Kaye H. 42:196-198.
Hill, Bob G. *See* Drake, Carl J. 24:83-92.
Hironaka, M. *See* Mosley, Jeffrey C. 49:241-248.
______. *See* Smith, Stuart D. 47:299-307.
Hixson, S. E., R. F. Walker, and C. M. Skau. Spring denitrification rates in soils of four eastside Sierra Nevada plant communities. 48:558-562.
Hoff, C. Clayton. Some heterosphyronid pseudoscorpions from New Mexico. 12:39-45.
Holmes, Jennifer A., David S. Dobkin, and Bruce A. Wilcox. Second nesting record and northward advance of the Great-tailed Grackle (*Quiscalus mexicanus*) in Nevada. 45:483-484.
Holomuzki, Joseph R. Predatory behavior of larval *Ambystoma tigrinum nebulosum* on *Limnephilus* (Trichoptera) larvae. 43:475-476.
Hoopes, Keith H. *See* Andersen, Ferron L. 29:35-41.
______. *See* Fox, J. Carl 30:131-145.
Horner, N. V. *See* Seiler, G. J. 47:280-282.
Hornig, C. Evan and Merlyn A. Brusven. Effects of suspended sediment on leaf processing by *Hesperophylax occidentalis* (Trichoptera: Limnephilidae) and *Pteronarcys californica* (Plecoptera: Pteronarcidae). 46:33-38.
Hottes, F. C. The description of the alate form of *Lachnus montanus* (Wilson). 14:21-22.
______. A new species of *Cinara* from Colorado (Aphididae). 21:17-19.
______. A new species of *Cinara* from Delaware (Aphididae). 21:20-22.
______. A note to commemorate the one-hundredth anniversary of Koch's Die Pflanzenlause. 14:79-82.
______. Notes on two little known aphid papers published by Luigi Macchiati. 12:55-57.
______. A review and key of North American *Cinara* (Homoptera: Aphididae) occurring on *Picea*. 21:35-50.
______. Some observations on the rostrum of *Cinara puerca* Hottes (Aphidae). 14:83-86.
______. Two new species of Lachnini (Aphididae) from Colorado. 12:57-61.
______ and G. F. Knowlton. Two new species of *Cinara* (Aphidae). 14:11-13.
______. *See* Drake, C. J. 10:51-61; 11:43-46; 12:35-38.
House, Donna. *See* Ehleringer, James 44:133-139.
Hovingh, Peter. Biogeographic aspects of leeches, mollusks, and amphibians in the Intermountain Region. 46:736-744.
______, Bob Benton, and Dave Bornholdt. Aquatic parameters and life history observations of the Great Basin spadefoot toad in Utah. 45:22-30.

______. *See* Worthylake, Kathleen Muriel. 49:364-372.
Howe, Frank P. and Lester D. Flake. Mourning Dove use of man-made ponds in a cold-desert ecosystem in Idaho. 49:627-631.
Howell, J. Franklin. Arthropod consortes of a kit fox den. 20:71-77.
______. A study of the aspectional variations of Siphonaptera associated with the nests of the Thomas wood rat *Neotoma lepida lepida* Thomas. 15:35-49.
Hsu, Sun Szen and Robert K. Vickery, Jr. The pattern of esterase variation in the *Mimulus glabratus* complex (Scrophulariaceae). 36:81-85.
Huang, Fu-sheng. *See* Wood, Stephen L. 46:465-467.
Huang, J., W. M. Hess, D. J. Weber, E. D. McArthur, S. E. Meyer, and R. Seegmiller. Computer analysis of cross sections of leaves of *Chrysothamnus* taxa and their relation to environmental conditions. 48:334-347.
Hubert, Wayne A. Survey of Wyoming crayfishes. 48:370-372.
______. *See* Anderson, Stanley H. 47:512-521.
______. *See* Parsons, Bradford G. 48:46-50.
Hudson, W. F. *See* Bragg, Arthur N. 11:87-90.
Hughes, Karen W. and Robert W. Vickery, Jr. Evolutionary divergence in closely related populations of *Mimulus guttatus* (Scrophulariaceae). 35:240-244.
Humphrey, L. David. Use of biomass predicted by regression from cover estimates to compare vegetational similarity of sagebrush-grass sites. 45:94-98.
Hungerford, C. Roger. *See* Germano, David J. 41:129-138.
Hunter, Katherine Bell. *See* Hunter, Richard 47:234-238.
Hunter, Richard. Competition between adult and seedling shrubs of *Ambrosia dumosa* in the Mojave Desert, Nevada. 49:79-84.
______, B. Turner, R. G. Lindberg, and Katherine Bell Hunter. Effects of land clearing on bordering winter annual populations in the Mohave Desert. 47:234-238.
Hupp, Jerry W., John T. Ratti, and Loren M. Smith. Gray Partridge foraging ecology in eastern South Dakota. 48:202-205.
Hutchings, John. *See* Bee, Robert G. 3:61-85.
Hutchins, Harry E. *See* Lanner, Ronald M. 44:357-360.
Hutchinson, Earl R. *See* Lanner, Ronald M. 32:171-175.

I

Igonoffo, Carlo M. Notes on louse-host associations of the Great Salt Lake Desert with keys to the lice. 16:9-17.
Infanger, Rex C. *See* Wadley, S. R. 42:67-72.
______. *See* Heckmann, Richard A. 44:75-82.
______. *See* Mickelsen, Roger W. 39:231-240.
Itzkowitz, Murray and W. L. Minckley. Qualitative behavior of a pupfish (*Cyprinodon atrorus*) in differing environments. 29:169-180.
Ivie, Michael A. *See* Gast, Sandra J. 49:381-385.

J

Jacobi, Gerald Z. and Richard W. Baumann. Winter stoneflies (Plecoptera) of New Mexico. 43:585-591.
Jacobi, W. R. *See* Zentz, W. R. 49:650-655.
Jacobson, Tracy L. C. and Bruce L. Welch. Planting depth of 'Hobble Creek' mountain big sagebrush seed. 47:497-499.
James, Hugo A. *See* Palmieri, James F. 36:97-100
Allen, James V. *See* St. Clair, Larry L. 41:317-332.
Jatkar, Shobha A., Samuel R. Rushforth, and Jack D. Brotherson. Diatom floristics and succession in a peat bog near Lily Lake, Summit County, Utah. 39:15-43.
Jehl, Joseph R., Jr. Biology of Red-necked Phalaropes (*Phalaropus lobatus*) at the western edge of the Great Basin in fall migration. 46:185-197.
______. *See* Paul, Don S. 50:299-302.
Jenkins, M. J. *See* Fredericks, S. E. 48:348-351.
______. *See* Cameron, D. E. 48:508-511.
Jenkins, M. Alan. *See* Mosher, James A. 38:438-446.
Jenkins, Michael J. Effect of western white pine cone production variability on mountain pine cone beetle population levels. 44:310-312.
______. Seed and cone insects associated with *Pinus monophylla* in the Raft River Mountains, Utah. 44:349-356.
Jenkins, Stephen H. *See* Mewaldt, William T. 46:577-580.
Jenni, Donald A. *See* Redmond, Roland L. 45:85-86.
Jennings, William, Loraine Yeatts, and Velma Richards. New records for *Monotropa hypopithys* (Ericaceae) from Colorado. 46:175-177.
Jensen, J. Neil. *See* Martin, Mark A. 45:677-687.
Jensen, James A. A fourth new sauropod dinosaur from the Upper Jurassic of the Colorado Plateau and sauropod bipedalism. 48:121-145.
______. New brachiosaur material from the Late Jurassic of Utah and Colorado. 47:592-608.
______. Three new sauropod dinosaurs from the Upper Jurassic of Colorado. 45:697-709.
______. Uncompahgre dinosaur fauna: a preliminary report. 45:710-720.
______. *See* Galton, Peter M. 33:129-132.
______. *See* Prothero, Donald R. 43:551-553.
Jensen, Lauritz A., Ferron L. Andersen, and Peter M. Schantz. The prevalence of *Echinococcus granulosus* and other taeniid cestodes in sheep dogs of central Utah. 42:65-66.
______, Jordan C. Pederson, and Ferron L. Andersen. Prevalence of *Elaeophora schneideri* and *Onchocerca cervipedis* in mule deer from central Utah. 42:351-352.
______. *See* Andersen, Ferron L. 46:208-216.

______. *See* Heckmann, Richard A. 47:355-372.

Jensen, Mark E. Applicability of the universal soil loss equation for southeastern Idaho wildlands. 43:579-584.

______. Soil characteristics of mountainous northeastern Nevada sagebrush community types. 49:469-481.

______. Some edaphic relations of southeastern Idaho wildlands. 44:265-271.

______, L. S. Peck, and M. V. Wilson. A sagebrush community type classification for mountainous northeastern Nevada rangelands. 48:422-433.

______, L. S. Peck, and M. V. Wilson. Vegetation characteristics of mountainous northeastern Nevada sagebrush community types. 48:403-421.

Johansen, Jeffrey R. and Samuel R. Rushforth. Cryptogamic soil crusts: seasonal variation in algal populations in the Tintic Mountains, Juab County, Utah. 45:14-21.

______ and Larry L. St. Clair. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA. 46:632-640.

______, Samuel R. Rushforth, and Jack D. Brotherson. Subaerial algae of Navajo National Monument, Arizona. 41:433-439.

______, Samuel R. Rushforth, and Irena Kaczmarska. Algal populations in Bottle Hollow Reservoir, Duchesne County, Utah. 42:205-218.

______. *See* Ashley, John 45:432-442.

______. *See* Brotherson, Jack D. 45:1-13.

______. *See* Rushforth, Samuel R. 40:98-100; 46:398-403; 48:324-326.

Johnson, D. Elmer. An albino swallow in Utah. 17:29.

______. A new *Cyrtopogon* (Asilidae, Diptera) from Utah. 3:1-4.

______. A new species of *Mallophora* from the Great Salt Lake Desert (Diptera: Asilidae). 18:41-42.

______ and Lucile M. Johnson. New and insufficiently known *Exoprosopa* from the Far West (Diptera: Bombyliidae). 18:69-84.

______ and Lucile M. Johnson. Taxonomic notes on North American beeflies with descriptions of new species (Diptera: Bombyliidae). 19:67-74.

______ and Lucile Maughan Johnson. New *Poecilanthrax*, with notes on described species (Diptera: Bombylidae). 17:1-26.

______ and Lucile Maughan Johnson. Notes on the genus *Bombylius* Linnaeus in Utah, with key and descriptions of new species (Diptera: Bombyliidae). 35:407-418.

______ and Lucile Maughan Johnson. Notes on the genus *Lordotus* Loew, with descriptions of new species (Diptera: Bombyliidae). 19:9-26.

______ and Lucile Maughan. Studies in Great Basin Bombyliidae. 13:17-27.

______. *See* Allred, Dorald M. 25:5-11.

Johnson, D. A. *See* Rumbaugh, M. D. 44:151-158.

Johnson, Donald R. *See* Gleason, Richard S. 45:81-84.

______. *See* Larrison, Earl J. 33:255-264.

______. *See* Nydegger, Nicholas C. 49:108-110.

Johnson, James B. *See* Furniss, Malcolm M. 47:375-382.

______. *See* Gast, Sandra J. 49:381-385.

______. *See* Stafford, Michael P. 46:287-293.

______. *See* Youtie, Berta A. 47:644-651.

Johnson, James E. Inventory of Utah crayfish with notes on current distribution. 46:625-631.

Johnson, John D. and Dorald M. Allred. Scorpions of Utah. 32:154-170.

Johnson, Lucile Maughan. *See* Johnson, D. Elmer 17:1-26; 18:69-84; 19:9-26; 19:67-74; 35:407-418.

Johnson, Mark K. Food of townsend ground squirrels on the Arid Land Ecology Reserve (Washington). 37:128.

______ and James G. MacCracken. Similarity between pronghorn and mule deer fecal pellets. 38:222-224.

Johnson, Ned K. Birds of the piñon association of the Kawich Mountains, Nevada. 16:32-33.

______. Notes on some Nevada birds. 14:15-18.

Johnson, Phyllis T. On the rodent-infesting Anoplura of Panama. 32:121-136.

Johnston, N. Paul. *See* Slaugh, Bartel T. 49:632-636; 50:379-380.

Jones, Kenneth H. *See* Mathiasen, Robert L. 43:741-746.

Jones, Stephen G. Preliminary survey of raptor species in the Manti Division, Manti-LaSal National Forest. 39:155-160.

Jordan, Lucy. *See* Austin, Dennis D. 49:159-166.

Jorgensen, C. D. *See* Croft, B. A. 37:366-374.

Jorgensen, Clive D. Disturbance of mammal traps by jack rabbits. 22:83-86.

______. A new species of *Spinibdella* from Utah (Bdellidae: Acarina). 27:98-101.

______. Oviposition habits of the tick *Dermacentor parumapertus* Neumann and factors influencing egg development. 17:42-51.

______ and Vichitra Mongkolprasith. Phytoseiid predators of mite pests in Utah apple orchards. 39:63-80.

______, Darin B. Allred, and Richard L. Westcott. Apple maggot (*Rhagoletis pomonella*) adaptation for cherries in Utah. 46:173-174.

______, H. Duane Smith, and James R. Garcia. Temporal activity patterns of *Dipodomys ordii* population. 40:282-286.

______. *See* Flake, Lester D. 29:143-149.

______. *See* Landeen, Dan S. 39:267-273.

______. *See* Leetham, John W. 29:96-104.

______. *See* Richins, Gary H. 34:105-120.

______. *See* Smith, H. Duane 38:215-221.

Jorgensen, Kent R. *See* Stevens, Richard 41:274-277.

Joyal, Elaine. New variety of *Oxytropis campestris* (Fabaceae) from the Columbia Basin, Washington. 50:373-377.

Judd, B. Ira. Vegetation zones around a small pond in the White Mountains of Arizona. 32:91-96.

______, James M. Laughlin, Herbert R. Guenther, and Royal Handegarde. The lethal decline of mesquite on the Casa Grande National Monument. 31:153-159.

K

Kaczmarska, Irena. *See* Johansen, Jeffrey 42:205-218.

______. *See* Rushforth, Samuel R. 44:120-124.

Kadlec, John A. *See* Smith, Loren M. 45:462-466.

Karp, Catherine A. and Harold M. Tyus. Humpback chub (*Gila cypha*) in the Yampa and Green rivers, Dinosaur National Monument, with observations on roundtail chub (*G. robusta*) and other sympatric fishes. 50:257-264.

Kass, Ronald J. A checklist of the vascular plants of the House Range, Utah. 48:102-116.

______ and Stanley L. Welsh. New species of *Primula* (Primulaceae) from Utah. 45:548-550.

Kaston, B. J. *See* Allred, Dorald M. 43:494-522.

Kay, Fenton R. Environmental responses of active lizards at Saratoga Springs, Death Valley, California. 30:146-165.

______. *Leptotyphlops humilis* in Death Valley, California. 30:91-93.

Kay, Jeanne. *See* Melanson, George P. 40:365-371.

Kay, P. A. and C. G. Oviatt. *Pinus longaeva* in the Stansbury Mountains, Utah. 38:49-50.

Keating, K. A. Bone chewing by Rocky Mountain bighorn sheep. 50:89.

Keegan, Hugh L. Collections of parasitic mites from Utah. 13:35-42.

Keller, Barry L. *See* Groves, Craig R. 44:468-470; 46:404-410.

______. *See* Mullican, Tim R. 47:276-279.

Kennedy, Joseph L. Seasonal growth of the tui chub, *Gila bicolor*, in Pyramid Lake, Nevada. 43:713-716.

______ and Paul A. Kucera. The reproductive ecology of the Tahoe sucker, *Catostomus tahoensis*, in Pyramid Lake, Nevada. 38:181-186.

Kennedy, Susan C. *See* Baker, William L. 45:747-777.

Key, Fenton R. An albino Pacific tree frog, *Hyla regilla*, from Death Valley, California. 29:111.

Khan, M. A., N. Sankhla, D. J. Weber, and E. D. McArthur. Seed germination characteristics of *Chrysothamus nauseosus* ssp. *viridulus* (Astereae, Asteraceae). 47:220-226.

______, D. J. Weber, and M. W. Hess. Elemental compartmentalization in seeds of *Atriplex triangularis* and *Atriplex confertifolia*. 47:91-95.

Killpack, Merlin L. and C. Lynn Hayward. New and unusual records of birds from the Uinta Basin, Utah. 18:23-25.

______. *See* Hayward, C. Lynn 18:26-30.

Kimball, Allen K. *See* Heckmann, Richard A. 47:13-21.

Kimball, John F. *See* Austin, Dennis D. 49:31-35.

King, J. *See* Austin, D. D. 44:572-574.

King, Michael M. and H. Duane Smith. Differential habitat utilization by the sexes of mule deer. 40:273-281.

King, Thomas Jackson, Jr. Late Pleistocene-early Holocene history of coniferous woodlands in the Lucerne Valley region, Mohave Desert, California. 36:227-238.

Klott, James H. and Frederick G. Lindzey. Comparison of sage and sharp-tailed grouse leks in south central Wyoming. 49:275-278.

Knick, Steven T., Steven J. Sweeney, J. Richard Alldredge, and J. David Brittell. Autumn and winter food habits of bobcats in Washington state. 44:70-74.

Knight, Dennis H. *See* Lichvar, Robert W. 45:734-746.

Knight, Harry H. *Tannerocoris* new genus, and new species of Miridae (Hemiptera) from the western United States. 30:227-231.

Knopf, F. L. and V. C. Bachman. Birds of Gunnison and Cub islands, Great Salt Lake, Utah. 37:247-251.

Knowles, Craig J. Reproductive ecology of black-tailed prairie dogs in Montana. 47:202-206.

______. Some relationships of black-tailed prairie dogs to livestock grazing. 46:198-203.

Knowlton, George F. Aphids from Mount Timpanogos, Utah. 3:5-8.

______. Aphids from Mt. Timpanogos, Utah, Part 2. 7:1-6.

______. Dodder aphids. 8:36.

______ and F. C. Harmston. Insect food of the Rock Wren. 3:22.

______ and D. R. Maddock. Insect food of the Western Meadowlark. 4:101-102.

______. *See* Hottes, F. C. 14:11-13.

______. *See* Wray, D. L. 13:43-46; 16:1-6; 16:7-8.

Knutson, Donald. *See* McKee, Arthur 47:163-167.

Koenig, Ervon R., John R. Baker, Larry J. Paulson, and Richard W. Tew. Limnological status of Big Soda Lake, Nevada, October 1970. 31:106-108.

Koestner, E. J. An annotated list of mammals collected in Nuevo Leon, Mexico, in 1938. 2:9-15.

Kohls, Glen M. A record of the occurrence of the tick *Ixodes muris* Bishopp and Smith on muskrats in Utah. 12:65-66.

______. *See* Brinton, Elias P. 23:166.

Koniak, Susan. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. 45:556-566.

______. Tree densities on pinyon-juniper woodland sites in Nevada and California. 46:178-184.

______. *See* Everett, Richard L. 41:467-475.

Korhel, Art H. and Tim W. Clark. Bald Eagle winter survey in the Snake River Canyon, Wyoming. 41:461-464.

Kratz, A. M. *See* Bourgeron, P. S. 48:301-323.

Krebill, Richard G. *See* Nelson, David L. 41:184-191; 42:262-272.

Krogh, John E. *See* Tanner, Wilmer W. 33:133-146.

Kucera, Paul A. Reproductive biology of the tui chub,

Gila bicolor, in Pyramid Lake, Nevada. 38:203-207.

______. *See* Kennedy, Joseph L. 38:181-186.

______. *See* Sigler, William F. 43:1-29.

______. *See* Vigg, Steven 41:278-289.

Kunzler, D. B. *See* Kunzler, L. M. 41:147-153.

Kunzler, L. M. and K. T. Harper. Recovery of Gambel oak after fire in central Utah. 40:127-130.

______, K. T. Harper, and D. B. Kunzler. Compositional similarity within the oakbrush type in central and northern Utah. 41:147-153.

Kurczewski, Frank E. *See* Elliott, Nancy B. 45:293-298.

L

La Rivers, Ira. The cerambycoid semi-aquatic Coleoptera of the Nevada area. 11:97-104

______. A new *Ambrysus* from Venezuela (Hemiptera, Naucoridae). 30:1-4.

______. Notes on the Histeridae (Coleoptera) known to occur in Nevada. 7:7-9.

______. The staphylinoid and dascilloid aquatic Coleoptera of the Nevada area. 10:66-70.

Lamarra, Marianne C. *See* Lamarra, Vincent A. 45:127-140.

Lamarra, Vincent, Marianne C. Lamarra, and John G. Carter. Ecological investigation of a suspected spawning site of Colorado squawfish on the Yampa River, Utah. 45:127-140.

______, Chuck Liff, and John Carter. Hydrology of Bear Lake Basin and its impact on the trophic state of Bear Lake, Utah-Idaho. 46:690-705.

Landeen, Dan S., Clive D. Jorgensen, and H. Duane Smith. Competition between harvester ants and rodents in the cold desert. 39:267-273.

Landers, James E. *See* Mpoame, Mbida 41:445-448.

Lanner, Harriette A. *See* Lanner, Ronald M. 44:357-360.

Lanner, Ronald M. Conifers of the Bear Lake area and mountains south of the Great Salt Lake. 31:85-89.

______. Effectiveness of the seed wing of *Pinus flexilis* in wind dispersal. 45:318-320.

______. A self-pollination experiment in *Pinus edulis*. 40:265-267.

______ and James A. Bryan. Association of Rhabdocline needle blight and epicormic branching in Douglas-fir. 41:476-477.

______ and James A. Bryan. Terminal bud formation in limber pine. 40:190-192.

______ and Earl R. Hutchinson. Relict stands of pinyon hybrids in northern Utah. 32:171-175.

______ and Ronald Warnick. Conifers of the San Francisco Mountains, San Rafael Swell, and Roan Plateau. 31:177-180.

______, Harry E. Hutchins, and Harriette A. Lanner. Bristlecone pine and Clark's Nutcracker: probable interaction in the White Mountains, California. 44:357-360.

Larrison, Earl J. and Donald R. Johnson. Density changes and habitat affinities of rodents of shadscale and sagebrush associations. 33:255-264.

Larsen, John H., Jr. *See* Miller, Brian T. 46:299-301.

Larsen, Kenneth. A fossil turtle from the Green River formation in Utah. 30:13-15.

______ and Wilmer W. Tanner. Numeric analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. 34:1-41.

______. *See* Smith, Hobart M. 33:276; 34:42-44; 34:94-96.

Larson, Frederic R. *See* Clary, Warren P. 44:627-634.

Lauck, David R. *See* Drake, Carl J. 19:43-52.

Laughlin, James M. *See* Judd, B. Ira 31:153-159.

Laundré, John W. Horizontal and vertical diameter of burrows of five small mammal species in southeastern Idaho. 49:646-649.

Laurance, William F., and Timothy D. Reynolds. Confirmation and expansion of the reported distribution of two species of Idaho herptiles. 44:313-316.

______. *See* Reynolds, Timothy D. 45:291-292.

Laven, Richard D. *See* Zimmerman, G. Thomas 47:652-659.

Lavin, Matt. Distribution of the moss family Grimmiaceae in Nevada. 42:583-588.

______. Floristics of the upper Walker River, California and Nevada. 43:93-130.

LaVoie, G. Keith, Howard P. Tietjen, and Michael W. Fall. Albinism in *Thomomys talpoides* from Colorado. 31:181.

Lawhead, David N. *See* Germano, David J. 46:711-720.

Lawson, C. S. Stilt Sandpiper and Hudsonian Godwit in Nevada. 37:532.

LeaMaster, Brad R. *See* Green, Jeffrey S. 45:567-570.

Lederer, Roger J. Fluctuation of a marsh habitat and the reproductive strategy of the Yellow-headed Blackbird. 38:85-88.

Lee, M. A. B. and Timothy Brothers. Seed dispersal in hybrid *Salsola*. 41:370-376.

Leech, Hugh B. Vasco M. Tanner--a lifetime with beetles. 30:213-215.

Leetham, John W. and Clive D. Jorgensen. Overwintering phytoseiid mites in central Utah apple orchards. 29:96-104.

Lehner, Philip N. Coyote-badger associations. 41:347-348.

Leland, Harry V., Steven V. Fend, James L. Carter, and Albert D. Mahood. Composition and abundance of periphyton and aquatic insects in a Sierra Nevada, California, stream. 46:595-611.

Lemen, Cliff A. and Patricia W. Freeman. Competition for food and space in a heteromyid community in the Great Basin Desert. 47:1-6.

Leonard, R. L., E. D. McArthur, D. J. Weber, and B. W. Wood. Electrophoresis of isoenzymes of 16 western shrubs: technique development. 41:377-388.

Lepthien, Larry W. *See* Bock, Carl E. 35:269-272.

______. *See* Bock, Carl E. 36:111.

Lesica, Peter. Vegetation and flora of Pine Butte Fen, Teton County, Montana. 46:22-32.

Lessard, E. D. and J. M. Schmid. Emergence, attack densities, and host relationships for the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) in northern Colorado. 50:333-338.

Lester, James E. *See* Bartos, Dale L. 44:459-467.

Lewellen, Gale R. and David A. White. The yellow perch fisheries of Deer Creek Reservoir, Utah, with notes on parasitism by *Ligula intestinalis*. 31:169-176.

Li, C. Y., Chris Maser, and Harlan Fay. Initial survey of acetylene reduction and selected microorganisms in the feces of 19 species of mammals. 46:646-650.

______, Chris Maser, Zane Maser, and Bruce A. Caldwell. Role of three rodents in forest nitrogen fixation in western Oregon: another aspect of mammal-mycorrhizal fungus-tree mutualism. 46:411-414.

Lichvar, Robert W. Evaluation of *Draba oligosperma*, *D. pectinipila*, and *D. juniperina* complex (Cruciferae). 43:441-444.

______. Evaluation of varieties in *Stanleya pinnata* (Cruciferae). 43:684-686.

______ and Robert D. Dorn. Additions to the vascular flora of Montana and Wyoming. 42:413-414.

______, Ellen I. Collins, and Dennis H. Knight. Checklist of vascular plants for the Bighorn Canyon National Recreational Area, Wyoming and Montana. 45:734-746.

______, Robert D. Dorn, and Erwin F. Evert. New records for the vascular flora of Wyoming and Montana. 43:739-740.

______. *See* Hartman, Ronald L. 40:408-413.

Liff, Chuck. *See* Lamarra, Vincent 46:690-705.

Lindberg, R. G. *See* Hunter, Richard 47:234-238.

Linder, Allan D. *See* Guyer, Craig 45:607-614.

Linder, Raymond L. *See* Apa, Anthony D. 50:107-113.

______. *See* Deisch, Michele S. 50:347-353.

Lindsey, J. P. *See* Gilbertson, R. L. 35:288-304; 38:42-48.

Lindsey, Susan Lyndaker. *See* Green, Jeffrey S. 45:567-570.

Lindzey, Frederick G. *See* Klott, James H. 49:275-278.

______. *See* Pekins, Peter J. 49:229-232.

______. *See* Oedekoven, Olin O. 47:638-643.

Linkhart, Brian D. *See* Reynolds, Richard T. 44:49-51.

Littlefield, Carroll D. and Steven P. Thompson. History and status of the Franklin's Gull on Malheur National Wildlife Refuge, Oregon. 41:440-444.

Littlefield, Victoria M. *See* Pederson, Jordan C. 47:252-258.

Livingston, Stephanie D. *See* Grayson, Donald K. 49:392-395.

Livingstone, David. *See* Drake, Carl J. 24:27-30.

Llewellyn, Jeffrey B. Differential parasitism of *Peromyscus maniculatus* and *Peromyscus truei* by *Cuterebra* larvae. 38:51-54.

Lockard, Lawrence L. Some relationships between water fertility and egg production in brown trout (*Salmo trutta*) from Montana streams. 35:435-441.

______ and R. Randall Parsons. Some parasites of paddlefish (*Polyodon spathula*) from the Yellowstone River, Montana. 35:425-426.

______, R. Randall Parsons, and Barry M. Schaplow. Some relationships between internal parasites and brown trout from Montana streams. 35:442-448.

______. *See* Barber, Delbert R. 33:53-60.

Lockwood, Jeffrey A. *See* Christiansen, T. A. 49:134-139.

______. *See* Christiansen, Tim A. 49:456-460; 49:562-569; 49:570-586.

Loerch, J. Cameron. *See* Ralphs, Michael H. 49:419-424.

Loftis, Larry. *See* Mathiasen, Robert L. 47:161-162.

Long, Charles A. Significance of the late Pleistocene fauna from the Little Box Elder Cave, Wyoming, to studies of zoogeography of recent mammals. 31:93-105.

Looman, Sandra J. *See* Talbot, Stephen S. 48:382.

Loomis, Richard B. A new species of chigger (Acarina, Trombiculidae) from lizards of western North America. 24:13-17.

Loudenslager, Eric J. *See* Martin, Mark A. 45:677-687.

Loveless, Earl C. *See* Roby, Carlos Y. 37:259.

Lowe, Charles H. *See* Tanner, Wilmer W. 49:511-516.

Lowry, Elbert J. and Harold J. Egoscue. The ermine in western Utah. 28:47.

Lund, R. *See* Weaver, T. 42:73-76.

Lutz, R. Scott and John A. Crawford. Habitat use and selection and home ranges of Merriam's Wild Turkey in Oregon. 49:252-258.

M

MacCracken, James G. and Richard M. Hansen. Energy and protein content of coyote prey in southeastern Idaho. 46:274-276.

______ and Richard M. Hansen. Seasonal foods of coyotes in southeastern Idaho: a multivariate analysis. 42:45-49.

______, Daniel W. Uresk, and Richard M. Hansen. Burrowing Owl foods in Conata Basin, South Dakota. 45:287-290.

______, Daniel W. Uresk, and Richard M. Hansen. Plant community variability on a small area in southeastern Montana. 43:660-668.

______. *See* Johnson, Mark K. 38:222-224.

MacLaren, Patricia A., Stanley H. Anderson, and Douglas E. Runde. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. 48:548-553.

MacMahon, James A. *See* Andre, John B. 40:68-72.

______. *See* Briggs, George M. 42:50-59; 43:523-530.

______. *See* Schimpf, David J. 45:37-60.

Maddock, D. R. *See* Knowlton, G. F. 4:101-102.
Madsen, James H., Jr. *See* Nelson, Michael E. 46:415-420.
______. *See* Nelson, Michael E. 47:239-251.
Mahood, Albert D., Robert D. Thomson, and Charles R. Goldman. Centric diatoms of Lake Tahoe. 44:83-98.
______. *See* Leland, Harry V. 46:595-611.
Mahrdt, Clark R. *See* Tinkham, Ernest R. 34:203-206.
Main, John L. and Elray S. Nixon. Distributional aspects of *Pinus ponderosa* in northwestern Nebraska. 28:24-29.
Malanson, George P. Habitat and plant distributions in hanging gardens of the Narrows, Zion National Park, Utah. 40:178-182.
______ and David R. Butler. Transverse pattern of vegetation on avalanche paths in the northern Rocky Mountains, Montana. 44:453-458.
Malek, Mitra and Gary McCallister. Incidence of the leech *Helobdella stagnalis* on the Colorado River in west central Colorado. 44:361-362.
Marble, James R. and Kimball T. Harper. Effect of timing of grazing on soil-surface cryptogamic communities in a Great Basin low-shrub desert: a preliminary report. 49:104-107.
Marsh, Paul C. and W. L. Minckley. Management of endangered Sonoran topminnow at Bylas Springs, Arizona: description, critique, and recommendations. 50:265-272.
______ and W. L. Minckley. Observations on recruitment and ecology of razorback sucker: lower Colorado River, Arizona-California-Nevada. 49:71-78.
______, Thomas A. Burke, Bruce D. DeMarais, and Michael E. Douglas. First North American record of *Cichlasoma managuense* (Pisces: Cichlidae). 49:387-389.
Marti, Carl D. Barn Owl diet includes mammal species new to the island fauna of the Great Salt Lake. 46:307-309.
Martin, Mark A., Dennis K. Shiozawa, Eric J. Loudenslager, and J. Neil Jensen. Electrophoretic study of cutthroat trout populations in Utah. 45:677-687.
Martin, S. Clark. *See* Medina, Alvin L. 48:373-381.
Martin, Stephen J., Max H. Schroeder, and Howard Tietjen. Burrow plugging by prairie dogs in response to Siberian polecats. 44:447-449.
Maryland, H. F. *See* Bjerregaard, R. S. 44:327-337.
Maser, Chris and Ronald S. Rohweder. Winter food habits of cougars from northeastern Oregon. 43:425-428.
______ and Zane Maser. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. 48:358-369.
______ and Zane Maser. Mycophagy of red-backed voles, *Clethrionomys californicus* and *C. gapperi*. 48:269-273.
______ and Zane Maser. Notes on mycophagy in four species of mice in the genus *Peromyscus*. 47:308-313.
______. *See* Brown, Barbara A. 46:421-426.
______. *See* Li, C. Y. 46:411-414; 46:646-650.
______. *See* Perez Calvo, Javier G. 49:618-620.
______. *See* Toweill, Dale E. 45:77-80.
______. *See* Whitaker, John O., Jr. 45:67-76; 46:228-240.
Maser, Zane. *See* Li, C. Y. 46:411-414.
______. *See* Maser, Chris 47:308-313; 48:269-273; 48:358-369.
______. *See* Perez Calvo, Javier G. 49:618-620.
Masslich, William J., Jack D. Brotherson, and Rex G. Cates. Relationships of aspen (*Populus tremuloides*) to foraging patterns of beaver (*Castor canadensis*) in the Strawberry Valley of central Utah. 48:250-262.
______. *See* Brotherson, Jack D. 45:535-541.
Mata, S. A. *See* Schmid, J. M. 46:445-448; 46:449-451.
Matherne, Anne. *See* Cushing, Bruce S. 40:193-195.
Mathiasen, Robert L. Infection of young Douglas-firs and spruces by dwarf mistletoes in the Southwest. 46:528-534.
______. Southern range extension of the white fir dwarf mistletoe in Arizona. 36:461-462.
______. Taxonomic studies of dwarf mistletoes (*Arceuthobium* ssp.) parasitizing *Pinus strobiformis*. 42:120-127.
______ and Frank G. Hawksworth. Distribution of limber pine dwarf mistletoe in Nevada. 50:91-92.
______ and Kenneth H. Jones. Range extensions for two dwarf mistletoes (*Arceuthobium* ssp.) in the Southwest. 43:741-746.
______ and Larry Loftis. Douglas-fir dwarf mistletoe parasitizing Pacific silver fir in northern California. 47:161-162.
______, Elizabeth A. Blake, and Carleton B. Edminster. Estimates of site potential for Douglas-fir based on site index for several southwestern habitat types. 46:277-280.
______, Elizabeth A. Blake, and Carleton B. Edminster. Estimates of site potential for ponderosa pine based on site index for several southwestern habitat types. 47:467-472.
______, Carleton B. Edminster, and Frank G. Hawksworth. Infection of young Douglas-firs by dwarf mistletoe in the Southwest. 50:67-71.
______, Frank G. Hawksworth, and Carleton B. Edminster. Effects of dwarf mistletoe on growth and mortality of Douglas-fir in the Southwest. 50:173-179.
______, Frank G. Hawksworth, and Carleton B. Edminster. Effects of dwarf mistletoe on spruce in the White Mountains, Arizona. 46:685-689.
______. *See* Hawksworth, Frank G. 38:89.
______. *See* Wagner, Michael R. 45:423-426.
Mathis, Wayne N. A systematic study of *Coenia* and

Paracoenia (Diptera: Ephydridae). 35:65-85.

Maughan, Lucile. *See* Johnson, D. Elmer 13:17-27.

Maughan, O. Eugene. Morphometry of sculpins (*Cottus*) in the Clearwater drainage, Idaho. 38:115-122.

______ and Gary E. Saul. Distribution of sculpins in the Clearwater River Basin, Idaho. 39:59-62.

Maupin, G. O. *See* Eads, R. B. 42:96-99.

Maxwell, Catherine S. *See* Morton, Martin L. 34:121-134.

McAda, Charles W. and Richard S. Wydoski. Growth and reproduction of the flannelmouth sucker, *Catostomus latipinnis*, in the Upper Colorado River Basin, 1975-76. 45:281-286.

McArthur, E. D. *See* Hegerhorst, D. F. 48:1-8.

______. *See* Huang, J. 48:334-347.

______. *See* Khan, M. A. 47:220-226.

______. *See* Leonard, R. L. 41:377-388.

McArthur, E. Durant and C. Lorenzo Pope. Karyotypes of four *Artemisia* species: *A. carruthii*, *A. filifolia*, *A. frigida*, and *A. spinescens*. 39:419-426.

______, Stewart C. Sanderson, and D. Carl Freeman. Isozymes of an autopolyploid shrub, *Atriplex canescens* (Chenopodiaceae). 46:157-160.

______, Charles F. Tiernan, and Bruce L. Welch. Subspecies specificity of gall forms on *Chrysothamnus nauseosus*. 39:81-87.

______. *See* Goodrich, Sherel 45:99-104.

______. *See* Welch, Bruce L. 46:281-286.

McArthur, J. V. *See* Barnes, James R. 46:204-207.

McArthur, J. Vaun and James R. Barnes. Patterns of macroinvertebrate colonization in an intermittent Rocky Mountain stream in Utah. 45:117-123.

McBee, Richard H. Varying prevalence of *Taenia taeniaeformis strobilocerci* in *Microtus pennsylvanicus* of Montana. 37:252.

McCallister, Gary. *See* Malek, Mitra 44:361-362.

______. *See* Orr, Thomas 47:345-346.

McComb, William C., James R. Sedell, and Todd D. Buchholz. Dam-site selection by beavers in an eastern Oregon basin. 50:273-281.

McCurdy, H. Dennis. *See* Andersen, Ferron L. 46:208-216.

McDaniel, Gregory. *See* Pekins, Peter J. 49:229-232.

McDonald, Jerry N. *Symbos cavifrons* (Artiodactyla: Bovidae) from Delta County, Colorado. 45:455-461.

McDonough, W. T. Revegetation of gopher mounds on aspen range in Utah. 34:267-275.

______, R. O. Harniss, and R. B. Campbell. Morphology of ephemeral and persistent leaves of three subspecies of big sagebrush grown in a uniform environment. 35:325-326.

McKee, Arthur and Donald Knutson. A disjunct ponderosa pine stand in southeastern Oregon. 47:163-167.

McKell, C. M. *See* Call, C. A. 44:363-371.

McKnight, Kent H. On two species of false morels (*Gyromitra*) in Utah. 31:35-47.

______. *See* Rooney, Hugh M. 32:181-189.

McLaughlin, Steven P. Floristic analysis of the southwestern United States. 46:46-65.

McMahon, Ellen E., Clifford C. Oakley, and Stephen P. Cross. First record of the spotted bat (*Euderma maculatum*) from Oregon. 41:270.

McMorris, J. Robert. Herpetological distribution and life history notes for Hawaii and western North America. 30:106-107.

McPherson, Guy R. *See* Britton, Carlton M. 50:115-120.

Mead, Emilee M. and Jim I. Mead. Snake Creek Burial Cave and a review of the Quaternary mustelids of the Great Basin. 49:143-154.

Mead, Jim I. *See* Mead, Emilee M. 49:143-154.

Medica, Philip A. Noteworthy mammal distribution records for the Nevada Test Site. 50:83-84.

______ and Rudolf G. Arndt. Opportunistic feeding in *Sceloporus horridus* from Jalisco, Mexico. 36:108-110.

______, Rudolf G. Arndt, and James R. Dixon. Additional records of reptiles from Jalisco, Mexico. 35:317-318.

______. *See* Smith, Donald D. 47:175-185.

Medin, Dean E. Birds of a shadscale (*Atriplex confertifolia*) habitat in east central Nevada. 50:295-298.

______. Breeding birds of an ancient bristlecone pine stand in east central Nevada. 44:272-276.

______. Grazing and passerine breeding birds in a Great Basin low-shrub desert. 46:567-572.

Medina, Alvin L. and S. Clark Martin. Stream channel and vegetation changes in sections of McKnight Creek, New Mexico. 48:373-381.

Medlyn, David A. and William D. Tidwell. New species of *Protocedroxylon* from the Upper Jurassic of British Columbia, Canada. 46:452-458.

______. *See* Tidwell, William D. 32:1-15; 33:61-76.

Meehan, William R., Merlyn A. Brusven, and John F. Ward. Effects of artificial shading on distribution and abundance of juvenile chinook salmon (*Oncorhynchus tshawytscha*). 47:22-31.

Melanson, George P. and Jeanne Kay. Flood frequency and the assemblage of dispersal types in hanging gardens of the Narrows, Zion National Park, Utah. 40:365-371.

Menkens, George E., Jr. *See* Shults, Larry M. 50:327-331.

Merkley, Gwen Shirley. *See* Rushforth, Samuel R. 48:154-179.

Mewaldt, William T. and Stephen H. Jenkins. Genetic variation of woodrats (*Neotoma cinerea*) and deer mice (*Peromyscus maniculatus*) on montane habitat islands in the Great Basin. 46:577-580.

Meyer, S. E. *See* Huang, J. 48:334-347.

Meyers, S. Mark. *See* Crawford, John A. 46:123-127.

Mickelsen, R. W. *See* Wadley, S. R. 42:67-72.

Mickelsen, Roger W., Richard A. Heckmann, and Rex C. Infanger. Potential use of Great Salt Lake water for

lobster culture. 39:231-240.
______. *See* Heckmann, Richard A. 44:75-82.
Millard, Jere B. *See* Halford, Douglas K. 38:64-70.
Miller, Brian T. and John H. Larsen, Jr. Feeding habits of metamorphosed *Ambystoma tigrinum melanostictum* in ponds of high pH (>9). 46:299-301.
Miller, Glenn C. *See* Wilt, F. Martin 48:228-231.
Miller, J. Scott. *See* Austin, George T. 42:232-240.
Miller, Richard F. and Leila M. Shultz. Development and longevity of ephemeral and perennial leaves on *Artemisia tridentata* Nutt. ssp. *wyomingensis*. 47:227-230.
______, Lee E. Eddleman, and Raymond F. Angell. Relationship of western juniper stem conducting tissue and basal circumference to leaf area and biomass. 47:349-354.
______. *See* Doescher, Paul S. 50:9-19.
Miller, Wade E. Late Pleistocene vertebrates of the Silver Creek local fauna from north central Utah. 36:387-424.
Milton, N. M. and T. L. Purdy. Plant and soil relationships in two hydrothermally altered areas of the Great Basin. 43:457-469.
Minckley, W. L. and Eric S. Gustafson. Early development of the razorback sucker, *Xyrauchen texanus* (Abbott). 42:553-561.
______. Records of atherinid fishes at inland localities in Texas and northern Mexico. 25:73-76.
______. *See* Itzkowitz, Murray 29:169-180.
______. *See* Marsh, Paul C. 49:71-78; 50:265-272.
______. *See* Schreiber, Donald C. 41:409-426.
______. *See* Tyus, Harold M. 48:25-30.
Minshall, G. W. *See* Newell, Robert L. 36:501-504.
Minshall, G. Wayne. *See* Newell, Robert L. 37:253-257; 38:55-58.
______. *See* Robinson, Christopher T. 50:303-311.
Mitchell, J. C. *See* Schmid, J. M. 44:575-578; 46:445-448; 46:449-451.
Mitchell, Ronald M. Breeding biology of the Double-crested Cormorant on Utah Lake. 37:1-23.
Modde, Timothy, Henry G. Drewes, and Mark A. Rumble. Effects of watershed alteration on the brook trout population of a small Black Hills stream. 46:39-45.
Mohanasundarum, M. *See* Drake, Carl J. 21:108-113.
Mohr, Carol O., D Elden Beck, and Elias P. Brinton. Observations on host-parasite relationships and seasonal history of ticks in San Mateo County, California. 24:1-6.
Mongkolprasith, Vichitra. *See* Jorgensen, Clive D. 39:63-80.
Monson, Stephen B. *See* Welch, Bruce L. 41:343-346.
Morden, C., Jack D. Brotherson, and Bruce N. Smith. Ecological differences of C_3 and C_4 plant species from central Utah in habitats and mineral composition. 46:140-147.
Moretti, Miles O. and Jack D. Brotherson. Vegetation and soil factors in the relation to slope position on foothill knolls in the Uinta Basin of Utah. 42:81-90.
Morris, Ronald L. and Wilmer W. Tanner. The ecology of the western spotted frog, *Rana pretiosa pretiosa* Baird and Girard, a life history study. 29:45-81.
Morton, Martin L. and John S. Gallup. Reproductive cycle of the Belding ground squirrel (*Spermophilus beldingi beldingi*): seasonal and age differences. 35:427-433.
______ and Robert J. Parmer. Body size, organ size, and sex ratios in adult and yearling Belding ground squirrels. 35:305-309.
______, Catherine S. Maxwell, and Charles E. Wade. Body size, body composition, and behavior of juvenile Belding ground squirrels. 34:121-134.
Mosher, James A., Clayton M. White, Joseph R. Murphy, and M. Alan Jenkins. Raptors of the Uinta National Forest, Utah. 38:438-446.
______. *See* Woffinden, Neil D. 39:253-254.
Mosley, Jeffrey C., Stephen C. Bunting, and M. Hironaka. Quadrat and sample sizes for frequency sampling mountain meadow vegetation. 49:241-248.
Mou-Sheng, Cheng and Samuel R. Rushforth. The algal flora of the campus of Brigham Young University, Provo, Utah. 37:402-406.
Mower, Kerry J. and H. Duane Smith. Diet similarity between elk and deer in Utah. 49:552-555.
Mpoame, Mbida and E. James Landers. *Ophiotaenia critica* (Cestoda: Proteocephalidae), a parasite of the Colorado River squawfish. 41:445-448.
Mulaik, Stanley. *See* Allred, Dorald M. 25:43-47
Mulaik, Stanley B. *See* Higgins, Harold G. 17:27-29.
Mullen, David A. and Robert C. Stebbins. An addition to the amphibian fauna of California. 38:429-437.
Mullican, Tim R. and Barry L. Keller. Burrows of the sagebrush vole (*Lemmiscus curtatus*) in southeastern Idaho. 47:276-279.
Muma, Martin H. *See* Allred, Dorald M. 31:164-168.
Munhall, Alan V. *See* Williams, Jack E. 50:243-248.
Murchison, Stuart. Utah chub (*Gila atraria*) from the latest Pleistocene Gilbert shoreline, west of Corrine, Utah. 49:131-133.
Murdock, Joseph R. *See* Welsh, Stanley L. 38:125-179.
Murphy, Dennis D. *See* Austin, George T. 47:186-201.
Murphy, Joseph R. *See* Ellis, David H. 29:165-167.
______. *See* Mosher, James A. 38:438-446.
______. *See* Smith, Dwight G. 42:395-404.
______. *See* Woffinden, Neil D. 37:411-425.
Murphy, Michael. *See* Rigby, J. Keith 36:206-210.
Murphy, Robert W. *See* Ottley, John R. 40:59-62.
Murvosh, Chad M. *See* Allen, Richard K. 47:283-286.

N

Nagy, Julius G. *See* Haufler, Jonathan B. 44:145-150.

Nambudiri, E. M. V. and M. K. Thomas. Effects of chemicals on the germination of pollen grains of *Torenia asiatica* Linn. 34:71-81.

______ and William D. Tidwell. *Syzygioxylon chhindwarense*, a new fossil wood from the Deccan Intertrappean series of India. 37:241-246.

______, W. D. Tidwell, and W. M. Hess. Ultrastructure of Eocene fossil plants. 41:161-166.

______, William D. Tidwell, and Shya Chitaley. Revision of *Sahniocarpon harrisii* Chitaley & Patil based on new specimens from the Deccan Intertrappean beds of India. 47:527-535.

Nash, Donald J. *See* Brunson, John T. 37:77-80.

______. *See* Hancock, Denis C., Jr. 42:597-598.

______. *See* Roberts, Patrick W. 40:141-142.

______. *See* Seaman, Richard N. 36:481-482.

______. *See* Wasserman, David 39:192-194.

Nebeker, G. *See* Brotherson, J. D. 38:19-30.

Nebeker, Glen T. Revision of the plant genus *Geranium* in Utah. 34:297-304.

Neely, E. E. *See* Shultz, L. M. 47:287-298.

Neely, Elizabeth E. and Alan T. Carpenter. Size, structure, and habitat characteristics of populations of *Braya humilis* var. *humilis* (Brassicaceae): an alpine disjunct from Colorado. 46:728-735.

Neese, E. *See* Welsh, S. L. 41:1-108.

Neese, Elizabeth and Stanley L. Welsh. A new species of *Penstemon* (Scrophulariaceae) from the Uinta Basin, Utah. 43:429-431.

______ and Stanley L. Welsh. New variety of *Yucca harrimaniae* (Agavaceae) from Utah. 45:789-790.

______. *See* Welsh, Stanley L. 43:373-374; 43:700.

Neese, Elizabeth C. New taxa and nomenclatural changes in Utah *Penstemon* (Scrophulariaceae). 46:459-460.

______. *See* Smith, Frank J. 49:461-465.

Neilson, Ronald P. and L. H. Wullstein. Microhabitat affinities of Gambel oak seedlings. 46:294-298.

Nelson, C. Riley. Robber flies of Utah (Diptera: Asilidae). 47:38-90.

______ and Richard W. Baumann. Systematics and distribution of the winter stonefly genus *Capnia* (Plecoptera: Capniidae) in North America. 49:289-363.

Nelson, D. L. *See* Bunderson, E. D. 46:427-440.

Nelson, David L. *Phalacropsis dispar* (Coleoptera: Phalacridae), an element in the natural control of native pine stem rust fungi in the western United States. 42:369-379.

______ and Richard G. Krebill. Occurence and effect of *Chrysomyxa pirolata* cone rust on *Picea pungens* in Utah. 42:262-272.

______ and Richard G. Krebill. A sagebrush wilt disease of unknown cause. 41:184-191.

Nelson, Michael A. *See* Baugh, Thomas M. 42:77-80.

Nelson, Michael E. Holocene predation of the Uinta ground squirrel by a badger. 50:385.

______ and James H. Madsen, Jr. Canids from the late Pleistocene of Utah. 46:415-420.

______ and James H. Madsen, Jr. Occurrence of the musk ox, *Symbos cavifrons*, from southeastern Idaho and comments on the genus *Bootherium*. 47:239-251.

Nelson, Rodger L., William S. Platts, and Osborne Casey. Evidence for variability in spawning behavior of interior cutthroat trout in response to environmental uncertainty. 47:480-487.

Newell, Robert. *See* Gaufin, Arden R. 34:45-59.

Newell, Robert L. and G. W. Minshall. An annotated list of the aquatic insects of southeastern Idaho. Part I: Plecoptera. 36:501-504.

______ and G. Wayne Minshall. An annotated list of the aquatic insects of southeastern Idaho, Part II: Trichoptera. 37:253-257.

______ and G. Wayne Minshall. An annotated list of the aquatic insects of southeastern Idaho, Part III: Ephemeroptera. 38:55-58.

Ng, David and James R. Barnes. Distributional study of the Zion snail, *Physa zionis*, Zion National Park, Utah. 46:310-315.

Nichols, Craig R. Evaluation of a program to control hydatid disease in central Utah. 43:65-72.

______. *See* Andersen, Ferron L. 46:208-216.

Nichols, D. W., H. D. Smith, and M. F. Baker. Rodent populations, biomass, and community relationships in *Artemisia tridentata*, Rush Valley, Utah. 35:191-202.

Nickerson, Max A. and H. L. Heringhi. Three noteworthy colubrids from southern Sonora, Mexico. 26:136-140.

Nielsen, Gerald L. *See* Tanner, Vasco M. 14:27-29.

Nielson, M. W. Additional new species of Teruliine leafhoppers with key to species (Cicadellidae: Coelidiinae: Teruliini). 49:398-403.

______. Genus *Paralidia* with descriptions of new species (Homoptera: Cicadellidae: Coelidiinae). 46:329-335.

______. New genera and new species of Neotropical Coelidiini (Homoptera: Cicadellidae: Coelidiinae). 48:232-249.

______. New genus and species of leafhopper in the tribe Tinobregmini (Homoptera: Cicadellidae: Coelidiinae). 46:134-136.

______. New oriental genus and species of leafhoppers in the tribe Coelidiini with descriptions of new species (Homoptera: Cicadellidae: Coelidiinae). 46:137-139.

______. New South American leafhoppers in the genus *Docalidia*, with a key to 37 species (Cicadellidae: Coelidiinae, Teruliini). 46:749-762.

______. New species of *Harasupia* with a revised key to the species (Homoptera: Cicadellidae: Coelidiinae). 49:233-240.

______. New thagriine leafhoppers from the Oriental Region, with a key to 30 species (Homoptera: Cicadellidae: Coelidiinae). 46:321-328.

______. On the genus *Paracarinolidia* (Cicadellidae:

Coelidiinae: Teruliini). 49:92-95.

______. Two new genera and two new species of teruliine leafhoppers (Homoptera: Cicadellidae: Coelidiinae). 49:96-99.

Nielson, Mervin W. New leafhopper species of *Coelidia* with a revised key and notes on homonymy and distribution (Homoptera: Cicadellidae, Coelidiinae). 43:669-674.

Nilsen, J. A. *See* Pritchett, C. L. 47:231-233.

Nixon, E. S. A mountain *Cercocarpus* population--revisited. 37:97-99.

Nixon, Elray S. A comparative study of the mountain brush vegetation in Utah. 27:59-66.

______. *See* Main, John L. 28:24-29.

Northstrom, Terry E. Typification and nomenclature of *Hedysarum boreale* Nutt. (Leguminosae). 36:458-460.

______ and Stanley L. Welsh. Revision of the *Hedysarum boreale* complex. 30:109-130.

Nydegger, Nicholas C. and Donald R. Johnson. Size and overlap of Townsend ground squirrel home ranges. 49:108-110.

O

O'Farrell, Michael J. Notes on the distribution of *Macrotus waterhousii* in southern Nevada. 30:53.

______ and William A. Clark. Notes on the white-tailed antelope squirrel, *Ammospermophilus leucurus*, and the pinyon mouse, *Peromyscus truei*, in north central Nevada. 44:428-430.

O'Kane, Steve L., Jr. Colorado's rare flora. 48:434-484.

O'Rourke, L. *See* Brotherson, J. D. 47:334-338.

Oakley, Clifford C. *See* McMahon, Ellen E. 41:270.

Oberndorfer, Reed Y. and Kenneth W. Stewart. The life cycle of *Hydroperla crosbyi* (Plecoptera: Perlodidae). 37:260-273.

Oedekoven, Olin O. and Fredrick G. Lindzey. Winter habitat-use patterns of elk, mule deer, and moose in southwestern Wyoming. 47:638-643.

Olsen, Eugene F. *See* Smith, Robert L. 36:385-386.

Olsen, O. Wilford and Clait E. Braun. New species of *Splendidofilaria* and *Chandlerella* (Filarioidea: Nematoda), with keys to the species, from the Band-tailed Pigeon (*Columba fasciata fasciata*) in the Rocky Mountain Region. 36:445-457.

Olson, M. Ray. *See* Slaugh, Bartel T. 49:632-636.

Olson-Rutz, Kathrin M., Philip J. Urness, and Laura A. Urness. Dam-raised fawns, an alternative to bottle feeding. 46:217-219.

Orr, Thomas and Gary McCallister. American swallow bug, *Oeciacus vicarius* Horvath (Hemiptera: Cimicidae), in *Hirundo rustica* and *Petrochelidon pyrrhonota* nests in west central Colorado. 47:345-346.

Ostrofsky, M. L. *See* Riley, L. E. 41:255-258.

Ottley, John R. A new subspecies of the snake *Lichanura trivirgata* from Cedros Island, Mexico. 38:411-416.

______ and Victor M. Velazques Solis. An extant, indigenous tortoise population in Baja California Sur, Mexico, with the description of a new species of *Xerobates* (Testudines: Testudinidae). 49:496-502.

______ and Wilmer W. Tanner. New range and a new subspecies for the snake *Eridiphas slevini*. 38:406-410.

______, Robert W. Murphy, and Geoffrey V. Smith. The taxonomic status of the rosy boa *Lichanura roseofusca* (Serpentes: Boidae). 40:59-62.

______. *See* Tanner, Wilmer W. 41:310.

Otto, Terry. *See* Heckmann, Richard 45:427-431.

Otto, Terry N. and Richard A. Heckmann. Host tissue response for trout infected with *Diphyllobothrium cordiceps* larvae. 44:125-132.

Oveson, Mark C. *See* Smith, H. Duane 46:542-546.

Oviatt, C. G. *See* Kay, P. A. 38:49-50.

Oviatt, Charles G. *See* Feduccia, Alan 46:547-548.

Owings, Donald H. and Mark Borchert. Correlates of burrow location in Beechey ground squirrels. 35:402-404.

P

Pack, Lloyd C, Jr. *See* Grogan, William L. 33:202.

Pack, Lloyd E., Jr. and Wilmer W. Tanner. A taxonomic comparison of *Uta stansburiana* of the Great Basin and the upper Colorado River basin in Utah, with a description of a new subspecies. 30:71-90.

Packham, Willis. *See* Tanner, Vasco M. 22:110-113.

Palmieri, James F. and Hugo A. James. The effects of leech behavior on penetration and localization of *Apatemon gracilis* (Trematoda: Strigeidae) cercariae and metacercariae. 36:97-100.

Palmieri, James R. Host-induced morphological variations in the strigeoid trematode *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). II. Body measurements and tegument modifications. 37:129-137.

______. Host-induced morphological variations in the strigeoid trematode *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). III. Organs of attachment. 37:375-382.

______. Host-induced morphological variations in the strigeoid trematode *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). IV. Organs of reproduction (ovary and testes), vitelline gland, and egg. 37:481-488.

______. Host-parasite relationships and intraspecific variation in *Posthodiplostomum minimum* (Trematoda: Diplostomatidae). 36:334-346.

______, Richard A. Heckmann, and R. Scott Evans. Life cycle and incidence of *Diplostomum spathaceum* Rudolphi (1819) (Trematoda: Diplostomatidae) in Utah. 36:86-96.

______. *See* Heckmann, Richard A. 38:473-477.

Parfitt, Bruce. *See* Baker, Marc A. 44:484-486.

Parker, Albert J. The successional status of *Cupressus arizonica*. 40:254-264.

______ and Kathleen C. Parker. Comparative successional roles of trembling aspen and lodgepole pine in the Southern Rocky Mountains. 43:447-455.

Parker, Kathleen C. *See* Parker, Albert J. 43:447-455.

Parmer, Robert J. *See* Morton, Martin L. 35:305-309.

Parrish, Jimmie R. *See* Ellis, Kevin L. 48:75-77; 49:404-407.

Parsons, Bradford G. and Wayne A. Hubert. Reproductive characteristics of two kokanee stocks in tributaries to Flaming Gorge Reservoir, Utah and Wyoming. 48:46-50.

Parsons, R. Randall. *See* Lockard, Lawrence L. 35:425-426; 35:442-448.

Patten, Duncan T. *See* Stromberg, Juliet C. 50:47-56.

Patterson, Craig. *See* Anderson, Stanley H. 47:512-521.

Patton, James L., Margaret F. Smith, Roger D. Price, and Ronald A. Hellenthal. Genetics of hybridization between the pocket gophers *Thomomys bottae* and *Thomomys townsendii* in northeastern California. 44:431-440.

Paul, Don S., Joseph R. Jehl, Jr., and Pamela K. Yochem. California Gull populations nesting at Great Salt Lake, Utah. 50:299-302.

Pauli, Andrew M. *See* Bleich, Vernon C. 48:563.

Paulson, L. J. *See* Axler, R. P. 38:187-192.

Paulson, Larry J. *See* Koenig, Ervon R. 31:106-108.

______. *See* Wilde, Gene R. 48:485-488.

Payne, K. Ellsworth. *See* Ferguson, Denzel E. 18:63-65.

Peabody, Frederick J. *Phlox longifolia* Nutt. (Polemoniaceae) complex of North America. 39:1-14.

Pearce, Richard C. and Wilmer W. Tanner. Helminths of *Sceloporus* lizards in the Great Basin and upper Colorado Plateau of Utah. 33:1-18.

Peck, L. S. *See* Jensen, M. E. 48:403-421.

______. *See* Jensen, M. E. 48:422-433.

Peck, Stewart B. Invertebrate faunas and zoogeographic significance of lava tube caves of Arizona and New Mexico. 42:405-412.

______. The invertebrate fauna of the caves of the Uinta Mountains, northeastern Utah. 41:207-212.

Pederson, Jordan C. Differential winter mortality between male and female mule deer fawns in Utah. 44:450-452.

______. Occurrence of ticks on mule deer in central Utah. 37:407-409.

______. Presence of maxillary canine teeth in mule deer in Utah. 43:445-446.

______ and K. T. Harper. Chemical composition of some important plants of southeastern Utah summer ranges related to mule deer reproduction. 39:122-128.

______ and R. Cary Tuckfield. A comparative study of coyote food habits on two Utah deer herds. 43:432-437.

______, R. C. Farentinos, and Victoria M. Littlefield. Effects of logging on habitat quality and feeding patterns of Abert squirrels. 47:252-258.

______. *See* Jensen, Lauritz A. 42:351-352.

______. *See* Welch, Bruce L. 48:274-279.

Pedretti, John W. *See* Baugh, Thomas M. 46:441-444.

______. *See* Taylor, Frances R. 49:491-495.

Pekins, Peter J., Frederick G. Lindzey, Jay A. Roberson, Gregory McDaniel, and Randy Berger. Winter habitats and foods of Blue Grouse in the Sheeprock Mountains, Utah. 49:229-232.

Pendlebury, George B. Second occurrence of the long-nosed snake, *Rhinocheilus lecontei lecontei*, in Idaho. 36:56.

Pendleton, Burton K. *See* Collins, Patrick D. 43:385-393.

Penrose, Richard L. *See* Barr, William F. 29:88-95.

Perez Calvo, Javier G., Zane Maser, and Chris Maser. Note on fungi in small mammals from the *Nothofagus* forest in Argentina. 49:618-620.

Pérez-Higareda, Gonzalo and Hobart M. Smith. Courtship behavior in *Rhinoclemmys areolata* from western Tabasco, Mexico (Testudines: Emydidae). 48:263-266.

Peters, Edward J. *See* Winger, Parley V. 32:211-219.

Peterson, B. V. The Simuliidae (Diptera) of Utah. Part I: Keys, original citations, types and distribution. 20:81-104.

______. *See* Theodor, O. 24:107-115.

Peterson, J. S. *See* Wilken, D. 44:516-517.

Peterson, Steven R. *See* Stauffer, Dean F. 46:117-122.

Petty, Jerold L. Bionomics of two aspen bark beetles, *Trypophloeus populi* and *Procryphalus mucronatus* (Coleoptera: Scolytidae). 37:105-127.

______. *See* Stewart, David A. 39:129-132.

Phillips, W. Levi. Rare aberrant forms of Utah *Cynthia*: the painted lady (Lepidoptera: Nymphylidae). 31:256-260.

Pietruszka, Robert D. Observations on seasonal variation in desert arthropods in central Nevada. 40:292-297.

Pimentel, Richard A. *See* Storm, Robert M. 9:59-63.

Pinkava, Donald J. *See* Baker, Marc A. 44:484-486.

Platt, Joseph B. A survey of nesting hawks, eagles, falcons, and owls in Curlew Valley, Utah. 31:51-65.

Platts, William S. *See* Nelson, Rodger L. 47:480-487.

Player, Rodney L. and Philip J. Urness. Habitat manipulation for reestablishment of Utah prairie dogs in Capitol Reef National Park. 42:517-523.

Pletsch, D. J. Anopheles mosquito records and observations in Montana. 7:23-28.

Poché, Richard M. New record of the bat *Plecotus phyllotis* from Utah. 35:452.

______ and Geoffrey L. Bailie. Notes on the spotted bat (*Euderma maculatum*) from southwest Utah. 34:254-256.

______ and George A. Ruffner. Roosting behavior of male *Euderma maculatum* from Utah. 35:121-122.

Polhemus, John T. The *austrina* group of the genus

Microvelia (Hemiptera: Veliidae). 34:207-217.

______. Notes concerning Mexican Saldidae, including the description of two species (Hemiptera). 32:137-153.

______. Notes on aquatic and semiaquatic Hemiptera from the southwestern United States (Insecta: Hemiptera). 33:113-119.

______ and Martin S. Polhemus. Aquatic and semiaquatic Heteroptera of the Grand Canyon (Insecta: Hemiptera). 36:221-226.

______ and Milton W. Sanderson. *Microvelia rasilis* Drake in Arizona: A species new to the United States (Heteroptera: Veliidae). 47:660.

Polhemus, Martin S. *See* Polhemus, John T. 36:221-226.

Poole, Stephen C., Verle R. Bohman, and James A. Young. Review of selenium in soils, plants, and animals in Nevada. 49:201-213.

Pope, C. Lorenzo. *See* McArthur, E. Durant 39:419-426.

Porter, J. Mark. *See* Heil, Kenneth D. 49:100-103.

Porter, Richard D. *See* Pritchett, Clyde L. 40:303-350.

______. *See* White, Clayton M. 43:717-727.

Ports, Lois K. *See* Ports, Mark A. 49:123-130.

Ports, Mark A. and Sarah B. George. *Sorex preblei* in the northern Great Basin. 50:93-95.

______ and Lois K. Ports. Associations of small mammals occurring in a pluvial lake basin, Ruby Lake, Nevada. 49:123-130.

Powell, J. *See* Christiansen, T. A. 49:134-139.

Powell, Jeff. *See* Christiansen, Jeffrey A. 49:456-460.

______. *See* Christiansen, Tim A. 49:562-569; 49:570-586.

Powers, Arnold L. and Benjamin H. Banta. Description of a *Phyllorhynchus* from Cerralvo Island, Gulf of California, Mexico. 34:241-244.

Price, K. P. and J. D. Brotherson. Habitat and community relationships of cliffrose (*Cowania mexicana* var. *stansburiana*) in central Utah. 47:132-151.

______. *See* Brotherson, J. D. 47:334-338.

Price, Kevin P. *See* Brotherson, Jack D. 44:317-323.

Price, Roger D. *See* Patton, James L. 44:431-440.

Prigge, B. *See* Thompson, H. 46:549-554.

Prigge, Barry A. New species of *Mentzelia* (Loasaceae) from Grand County, Utah. 46:361-365.

Pritchett, C. L., J. A. Nilsen, M. P. Coffeen, and H. D. Smith. Pygmy rabbits in the Colorado River drainage. 47:231-233.

Pritchett, Clyde L., Richard D. Porter, and Benjamin W. Wood. Terrestrial vertebrate fauna of the Kaiparowits Basin. 40:303-350.

______. *See* Belk, Mark C. 50:387-389.

______. *See* Dobson, Martin L. 47:551-561.

______. *See* Smith, H. Duane 46:542-546.

Prothero, Donald R. and James A. Jensen. A mammalian humerus from the Upper Jurassic of Colorado. 43:551-553.

Provonsha, A. The Zygoptera (Odonata) of Utah with notes on their biology. 35:379-390.

Purdy, T. L. *See* Milton, N. M. 43:457-469.

Pyrah, Grant L. *Agropyron arizonicum* (Gramineae: Triticeae) and a natural hybrid from Arizona. 43:131-136.

R

Rader, R. T. *See* Cushing, C. E. 41:431-432.

Rader, Russell B. and James V. Ward. Mayfly growth and population density in constant and variable temperature regimes. 50:97-106.

Ragenovich, I. *See* Schmid, J. M. 41:465-466.

Ralphs, M. H. and V. L. Bagley. Population cycles of Wahweap milkvetch on the Henry Mountains and seed reserve in the soil. 48:541-547.

Ralphs, Michael H., Brock Benson, and J. Cameron Loerch. Soil-site relationships of white locoweed on the Raft River Mountains. 49:419-424.

Rampton, Calvin L. Vasco M. Tanner--a public servant. 30:195.

Ramsay, M. John. *See* Andersen, Ferron L. 47:207-219.

Ranasinghe, M. A. S. K. Bionomics of a subterranean gall midge (Diptera: Cecidomyiidae) from *Artemisia ludoviciana*. 37:429-442.

Raphael, Martin G. *See* Henry, Stephen E. 50:381-383.

Rasmussen, Lars L. and Jack D. Brotherson. Response of winterfat (*Ceratoides lanata*) communities to release from grazing pressure. 46:148-156.

______. *See* Brotherson, Jack D. 46:348-357.

Ratliff, Raymond D. Nutrients in *Carex exserta* sod and gravel in Sequoia National Park, California. 45:61-66.

______ and Stanley E. Westfall. Dry-year grazing and Nebraska sedge (*Carex nebraskensis*). 47:422-426.

Ratti, John T. *See* Hupp, Jerry W. 48:202-205.

Rechel, E. A. and W. F. Campbell. The effects of radiation from uranium mill tailings on *Tradescantia*. 38:456-462.

Redder, Alan J. *See* Anderson, Stanley H. 47:512-521.

Redmond, Roland L. and Donald A. Jenni. Note on the diet of Long-billed Curlew chicks in western Idaho. 45:85-86.

Reese, Kerry P. Three additional cases of predation by magpies on small mammals. 45:152-153.

Reid, William H. Germination of *Pinus aristata* Engelm. 32:235-237.

______, Pamela Sensiba, and C. Edward Freeman. A mixed pollination system in *Penstemon pseudospectablis* M. E. Jones (Scrophulariaceae). 48:489-494.

Resh, Vincent H. and Mark A. Barnby. Distribution of shore bugs and shore flies at Sylvan Springs, Yellowstone National Park. 44:99-103.

Reveal, James L. Annotated key to *Eriogonum* (Polygonaceae) of Nevada. 45:493-519.

______. Comments on *Lesquerella hitchcockii*. 30:94-98.

______. Comments on two names in an early Utah flora.

32:221-222.

______. *Eriogonum divaricatum* Hook (Polygonaceae), an intermountain species in Argentina. 41:143-146.

______. Five new varieties of *Eriogonum* (Polygonaceae). 32:113-116.

______. The genus *Eriogonum* Michx. (Polygonaceae) and Michel Gandoger. 40:143-148.

______. *Ilex rushforthii*, a new name. 31:189.

______. A new combination in *Penstemon* (Scrophulariaceae). 34:311.

______. A new name for a Utah *Lepidium*. 27:177-181.

______. New Nevada entities and combinations in *Eriogonum* (Polygonaceae). 45:276-280.

______. A new pulvinate *Eriogonum* (Polygonaceae) from Utah. 41:229-231.

______. A new subfruticose *Eriogonum* (Polygonaceae) from western Colorado. 33:120-122.

______. A new variety of *Eriogonum umbellatum* from southern Nevada. 28:157-159.

______. Notes on *Eriogonum* - III: On the status of *Eriogonum pauciflorum* Pursh. 27:102-117.

______. Notes on *Eriogonum* - V: A revision of the *Eriogonum corymbosum* complex. 27:183-229.

______. A revision of the Utah species of *Townsendia* (Compositae). 30:23-52.

______. Two new varieties of *Eriogonum* (Polygonaceae) from the intermountain region. 34:245-246.

______. Types of Nevada buckwheats (*Eriogonum*: Polygonaceae). 45:488-492.

______. *Wislouchiella planctonica* Skvortz. (Chlorophyta, Volvocales), a new algal record for Nevada. 29:43.

______ and Janice C. Beatley. A new variety of *Penstemon thurberi* (Scrophulariaceae). 34:230.

______ and Barbara J. Ertter. Reestablishment of *Stenogonum* Nutt. (Polygonaceae). 36:272-280.

______ and Eloise L. Styler. Miscellaneous chromosome counts of western American plants-II. 33:19-25.

______. *See* Hess, William J. 36:281-333.

______. *See* Strachan, Jeffrey L. 41:198-200.

______. *See* Welsh, Stanley L. 35:327-376; 37:279-365.

Reynolds, Richard T. and Brian D. Linkhart. Methods and materials for capturing and monitoring Flammulated Owls. 44:49-51.

Reynolds, Timothy D. Pronghorn responses to hunting coyotes. 43:88-92.

______. Response of reptile populations to different land management practices on the Idaho National Engineering Laboratory Site. 39:255-262.

______ and William F. Laurance. Addendum to the distribution of two herptiles in Idaho. 45:291-292.

______ and Trent D. Stephens. Multiple ectopic limbs in a wild population of *Hyla regilla*. 44:166-169.

______, John W. Connelly, Douglas K. Halford, and W. John Arthur. Vertebrate fauna of the Idaho National Environmental Research Park. 46:513-527.

______. *See* Laurance, William F. 44:313-316.

______. *See* Seeley, Rodney R. 49:556-561.

______. *See* Stephens, Daniel A. 43:728-738.

Richards, Gerald. Wintering habits of some birds at the Nevada atomic test site. 22:30-31.

Richards, Gerald L. Prairie Falcon imitates flight pattern of the Loggerhead Shrike. 25:48.

Richards, Velma. *See* Jennings, William 46:175-177.

Richins, Gary H., H. Duane Smith, and Clive D. Jorgensen. Growth and development of the western harvest mouse, *Reithrodontomys megalotis megalotis*. 34:105-120.

______. *See* Ellis, Kevin L. 49:404-407.

______. *See* Smith, H. Duane 38:215-221.

Rickard, Lora G. *See* Shults, Larry M. 45:604-606.

Rickart, Eric A. Type specimens of recent mammals in the Utah Museum of Natural History, University of Utah. 47:620-624.

Rigby, J. Keith and James K. Gilland. A new fossil sponge from the Ordovician Garden City limestone of southeastern Idaho. 37:475-480.

______ and Michael Murphy. *Hindia sphaeroidalis* Duncan from the Devonian of Nevada (Porifera). 36:206-210.

Riggs, Robert A. *See* Austin, Dennis D. 49:31-35.

Righetti, Timothy. *See* Baker, Marc A. 44:484-486.

Riley, L. E. and M. L. Ostrofsky. The effect of elevated temperature on copper toxicity to the thermophilic alga *Synechococcus lividus* (Cyanophyceae). 41:255-258.

Rinne, John N. Effects of livestock grazing exclosure on aquatic macroinvertebrates in a montane stream, New Mexico. 48:146-153.

Ripley, J. D. Plants of Angel Island, Marin County, California. 40:385-407.

Risser, Arthur C., Jr. *See* Blaustein, Andrew R. 34:312-316.

Roberson, Jay A. *See* Pekins, Peter J. 49:229-232.

______. *See* Slaugh, Bartel T. 49:632-636; 50:379-380.

Roberts, David W. *See* Hallsten, Gregory P. 48:352.

Roberts, Patrick W., Donald J. Nash, and Robert E. Keiss. Transferrin polymorphism in bighorn sheep, *Ovis canadensis*, in Colorado. 40:141-142.

Robey, Edward H., Jr., H. Duane Smith, and Mark C. Belk. Niche pattern in a Great Basin rodent fauna. 47:488-496.

Robins, C. Richard. *See* Courtenay, Walter R., Jr. 47:523-526.

Robinson, Christopher T. and G. Wayne Minshall. Longitudinal development of macroinvertebrate communities below oligotrophic lake outlets. 50:303-311.

______ and Samuel R. Rushforth. Diatom flora of Mink Creek, Idaho, USA. 49:155-158.

Robinson, James V. Size and seasonal activity patterns of abundant sympatric spider species in Cache County, Utah. 44:104-110.

Robison, W. Gerald, Jr. *See* Tanner, Wilmer W. 19:75-82.

Roby, Carlos Y. and Earl C. Loveless. Range extension of *Trionyx spiniferus emoryi* into Utah (Reptilia). 37:259.

Roby, Kenneth B. *See* Erman, Don C. 37:57-66.

Rodriguez, Ronald L. *See* Welch, Bruce L. 48:274-279.

Rogers, C. E. *See* Seiler, G. J. 47:280-282.

Rohweder, Ronald S. *See* Maser, Chris 43:425-428.

Romney, E. M. *See* Farnsworth, R. B. 36:65-80.

Romo, James T. and Marshall R. Haferkamp. Effects of osmotic potential, potassium chloride, and sodium chloride on germination of greasewood (*Sarcobatus vermiculatus*). 47:110-116.

Rooney, Hugh M. and Kent H. McKnight. Aquatic Phycomycetes of Lily Lake, Utah. 32:181-189.

Roper, Paul R. *See* Andersen, Ferron L. 35:203-230.

Roscoe, Ernest J. Additional records of *Helix aspersa* Muller from Utah. 14:90.

______. Escalante and the recognition of ancient lakes in the Great Basin. 22:87-88.

______. Some terrestrial gastropods from the Deep Creek Mountains, Juab County, Utah. 14:19.

______ and Lottie O. Roscoe. The type locality of *Triodopsis cragini* Call (Pulmonata: Polygyridae). 14:87-89.

Roscoe, Lottie O. *See* Roscoe, Ernest J. 14:87-89.

Rose, Jeff. *See* Doescher, Paul S. 50:9-19.

Rottman, Mary Lou and Emily L. Hartman. Tundra vegetation of three cirque basins in the northern San Juan Mountains, Colorado. 45:87-93.

______. *See* Hartman, Emily L. 47:152-160.

Roueche, William L. *See* Webb, Robert G. 31:193-212.

Roundy, Bruce A. *See* Young, James A. 46:1-21.

Rubink, William L. *See* Evans, Howard E. 38:59-63.

Ruffner, George A. *See* Poché, Richard M. 35:121-122.

Ruggiero, Leonard F. *See* Henry, Stephen E. 50:381-383.

Ruhoff, Florence A. *See* Drake, Carl J. 20:29-38; 20:80.

Rumbaugh, M. D. and D. A. Johnson. Nodulation and acetylene reduction by two legumes with rhizobia indigenous to northern Great Basin soils. 44:151-158.

Rumble, Mark A. Avian use of scoria rock outcrops. 47:625-630.

______. *See* Modde, Timothy 46:39-45.

Runde, Douglas E. *See* MacLaren, Patricia A. 48:548-553.

Rushforth, S. R. *See* Cushing, C. E. 44:421-427.

Rushforth, Samuel R. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. 43:73-78.

______ and Irena Kaczmarska. New records of diatoms from Blue Lake Warm Spring, Tooele County, Utah. 44:120-124.

______ and Gwen Shirley Merkley. Comprehensive list by habitat of the algae of Utah, USA. 48:154-179.

______ and Lorin E. Squires. New records and comprehensive list of the algal taxa of Utah Lake, Utah, USA. 45:237-254.

______, Sheril D. Burton, Jeffrey R. Johansen, and Judith A. Grimes. The bacterium *Thioploca ingrica* on wet walls in Zion National Park, Utah. 40:98-100.

______, Jeffrey R. Johansen, and Darwin L. Sorensen. Occurrence of *Phaedactylum tricornutum* in the Great Salt Lake, Utah, USA. 48:324-326.

______, Lorin E. Squires, and Jeffrey R. Johansen. Three new records for diatoms from the Great Basin, USA. 46:398-403.

______. *See* Ashley, John 45:432-442.

______. *See* Brotherson, Jack D. 45:1-13; 45:542-545; 47:583-591.

______. *See* Ekins, Laura 46:612-624.

______. *See* Grimes, Judith A. 40:223-228; 44:36-48.

______. *See* Jatkar, Shobha A. 39:15-43.

______. *See* Johansen, Jeffrey R. 41:433-439; 42:205-218; 45:14-21.

______. *See* Mou-Sheng, Cheng 37:402-406.

______. *See* Robinson, Christopher T. 49:155-158.

______. *See* Squires, Lorin E. 39:245-252.

______. *See* St. Clair, Larry L. 38:211-214; 41:317-332.

______. *See* Whiting, Mark C. 38:31-41.

Russell, Richard H. Mollusca of Fish Springs, Juab County, Utah: rediscovery of *Stagnicola pilsbryi* (Hemphill, 1890). 31:223-236.

Rust, R. W., L. M. Hanks, and R. C. Bechtel. Aculeata Hymenoptera of Sand Mountain and Blow Sand Mountains, Nevada. 43:403-408.

Rust, Richard W. Opportunistic foraging by the kangaroo rat *Dipodomys deserti* Stephens (Rodentia: Heteromyidae). 49:396-397.

Ryder, Ronald A. *See* Dunn, Peter O. 46:651-655.

S

Sanborn, Sherburn R. *See* Smith, Donald D. 47:175-185.

Sanders, Hermand O. The female genitalia and spermathecae of some of the Rhynchophora. 20:1-22.

Sanderson, Milton W. *See* Blinn, Dean W. 49:85-88.

______. *See* Polhemus, John T. 47:660.

Sanderson, Stewart C. *See* McArthur, E. Durant 46:157-160.

Sangster, Mary E. Spring waterfowl migration in the Uinta Basin of northeastern Utah. 37:274-278.

Sankhla, N. *See* Davis, Tim D. 45:520-526.

______. *See* Khan, M. A. 47:220-226.

Saul, Gary E. *See* Maughan, O. Eugene 39:59-62.

Saunders, Wayne E. Life history notes on *Parabacillus coloradus* Scud. 19:83.

Sawin, H. Lewis. *See* Smith, Hobart M. 35:100-102.

Sawyer, Thomas W., Lari M. Cowgill, and Ferron L. Andersen. Helminth parasites of cats and dogs from central Utah. 36:471-474.

Schantz, Peter M. Evaluation of a program to control hydatid disease in central Utah. 43:65-72.

______ and Ferron L. Andersen. Dog owners and

hydatid disease in Sanpete County, Utah. 40:216-220.

______. *See* Jensen, Lauritz A. 42:65-66.

Schaplow, Barry M. *See* Lockard, Lawrence L. 35:442-448.

Schimpf, David J. and Robert L. Bayn, Jr. Reproductive attributes of some Rocky Mountain subalpine herbs in successional context. 43:573-578.

______ and James A. MacMahon. Insect communities and faunas of a Rocky Mountain subalpine sere. 45:37-60.

______, Jan A. Henderson, and James A. MacMahon. Some aspects of succession in the spruce-fir forest zone of northern Utah. 40:1-26.

Schlising, Robert A. *See* Gut, Larry J. 37:523-529.

Schmid, J. M. Emergence of adult pandora moths in Arizona. 44:161-165.

______, P. A. Farrar, and I. Ragenovich. Length of western tent caterpillar egg masses and diameter of their associated stems. 41:465-466.

______, J. C. Mitchell, K. D. Carlin, and M. R. Wagner. Insect damage, cone dimensions, and seed production in crown levels of ponderosa pine. 44:575-578.

______, J. C. Mitchell, and S. A. Mata. Number and condition of seeds in ponderosa pine cones in central Arizona. 46:449-451.

______, J. C. Mitchell, and S. A. Mata. Ponderosa pine conelet and cone mortality in central Arizona. 46:445-448.

______. *See* Lessard, E. D. 50:333-338.

Schoener, Carol S. Notes on three varieties of *Astragalus lentiginosus* (Leguminosae). 34:180.

Schowalter, T. D., S. G. Stafford, and R. L. Slagle. Arboreal arthropod community structure in an early successional coniferous forest ecosystem in western Oregon. 48:327-333.

Schreiber, Donald C. and W. L. Minckley. Feeding interrelations of native fishes in a Sonoran Desert stream. 41:409-426.

Schreiber, R. Kent. Annual energy budgets for three common rodent species in the northern Great Basin. 39:143-154.

Schroeder, Max H. *See* Martin, Stephen J. 44:447-449.

Schultz, Vincent. References on Nevada Test Site ecological research. 26:79-86.

Schulz, Peter D. and Dwight D. Simons. Prehistoric bighorn sheep in the northern Sierra Nevada, California. 33:221-224.

Schumann, Paul B. *See* Deacon, James E. 47:538-546.

Schwartz, Orlando A. *See* Bleich, Vernon C. 35:62-64.

Scifres, C. J. *See* Whisenant, S. G. 44:558-562.

Scrivner, Jerry H. and H. Duane Smith. Pocket gophers (*Thomomys talpoides*) in successional stages of spruce-fir forest in Idaho. 41:362-367.

Seaman, Richard N. and Donald J. Nash. Variation in the incidence of botfly larvae (*Cuterebra*) in two sympatric species of *Peromyscus* in northern Colorado. 36:481-482.

______. *See* Brunson, John T. 37:77-80.

Sedell, James R. *See* McComb, William C. 50:273-281.

Seegmiller, R. *See* Huang, J. 48:334-347.

Seeley, Rodney R. and Timothy D. Reynolds. Effect of indomethacin-treated wheat on a wild population of montane voles. 49:556-561.

Seiler, G. J., G. Zolnerowich, N. V. Horner, and C. E. Rogers. Spider fauna of selected wild sunflower species sites in the southwest United States. 47:280-282.

Seiler, Gerald J. and Luka Cuk. Range extension of *Helianthus* spp. (Asteraceae) in Arizona and Utah. 41:393-394.

Sensiba, Pamela. *See* Reid, William H. 48:489-494.

Severson, K. E. and B. J. Hayward. Rodent weights in modified pinyon-juniper woodlands of southwestern New Mexico. 48:554-557.

Severson, Kieth. *See* Uresk, Daniel W. 48:353-357.

Severson, Kieth E. and Daniel W. Uresk. Influence of ponderosa pine overstory on forage quality in the Black Hills, South Dakota. 48:78-82.

Seville, Robert S. *See* Shults, Larry M. 50:327-331.

Shane, John D. and Kimball T. Harper. Influence of precipitation and temperature on ring, annual branch increment, and needle growth of white fir and Douglas-fir in central Utah. 39:219-225.

Shapiro, Arthur M. The alpine butterflies of Castle Peak, Nevada County, California. 37:443-452.

______. Genetics, environment, and subspecies differences: the case of *Polites sabuleti* (Lepidoptera: Hesperiidae). 35:33-38.

______. Montane insular butterfly biogeography: fauna of Ball Mountain, Siskiyou County, California. 46:336-347.

______. Photoperiodic responses of phenologically aberrant populations of pierid butterflies (Lepidoptera). 35:310-316.

______. Seasonal phenology and possible migration of the mourning cloak butterfly, *Nymphalis antiopa* (Lepidoptera: Nymphalidae), in California. 46:112-116.

Sharps, Jon C. and Daniel W. Uresk. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. 50:339-345.

______. *See* Uresk, Daniel W. 46:249-253.

Sharrow, Steven H. *See* Everett, Richard L. 45:105-112.

Shaw, Keith. Correction: *Rhamnus cathartica* L. is not *Prunus nigra* Ait. from Alberta. 38:123.

______. Flora of the Lee Creek Valley, Alberta. 39:277-283.

______. Unusual tooth wear in elk at Glacier National Park, Montana. 41:368-369.

Shaw, Richard J. *See* Spence, John R. 41:232-242; 43:483-491.

Shaw, Robert K. A taxonomic and ecologic study of the riverbottom forest on St. Mary River, Lee Creek, and Belly River in southwestern Alberta, Canada.

36:243-271.
Sheldon, Andrew L. Stonefly (Plecoptera) records from the basin ranges of Nevada and Utah. 39:289-292.
Shiozawa, Dennis K. *See* Devine, Michael G. 44:509-515.
______. *See* Martin, Mark A. 45:677-687.
Shirley, Dennis L. *See* White, Clayton M. 43:717-727.
Shook, Gary A. Checklist of tiger beetles from Idaho (Coleoptera: Cicindelidae). 44:159-160.
Short, Jeffrey A. *See* Heckmann, Richard A. 47:13-21.
Shryer, Jeff and Dennis L. Flath. First record of pallid bat (*Antrozous pallidus*) from Montana. 40:115.
Shults, Larry M., and Lora G. Rickard. Helminth parasites of the white-tailed jackrabbit, *Lepus townsendi*, from northwestern Colorado and southern Wyoming. 45:604-606.
______ and Nancy L. Stanton. Helminth parasites of the Wyoming ground squirrel, *Spermophilus elegans* Kennicott, 1863. 47:103-104.
______, Robert S. Seville, Nancy L. Stanton, and George E. Menkens, Jr. *Eimeria* sp. (Apicomplexa: Eimeriidae) from Wyoming ground squirrels, *Spermophilus elegans*, and white-tailed prairie dogs, *Cynomys leucurus*, in Wyoming. 50:327-331.
Shultz, L. M., and E. E. Neely, and J. S. Tuhy. Flora of the Orange Cliffs of Utah. 47:287-298.
Shultz, Leila M. *See* Miller, Richard F. 47:227-230.
Shupe, J. B. and Jack D. Brotherson. Differential effects of cattle and sheep grazing on high mountain meadows in the Strawberry Valley of central Utah. 45:141-149.
Sidner, Ronnie. *See* Davis, Russell 49:140-141.
______. *See* Duncan, Russell B. 50:197-200.
Sigler, J. W. and W. F. Sigler. History of fish hatchery development in the Great Basin states of Utah and Nevada. 46:583-594.
Sigler, W. F. *See* Sigler, J. W. 46:583-594.
Sigler, William F., William T. Helm, Paul A. Kucera, Steven Vigg, and Gar W. Workman. Life history of the Lahontan cutthroat trout, *Salmo clarki henshawi*, in Pyramid Lake, Nevada. 43:1-29.
______, Steven Vigg, and Mimi Bres. Life history of the cui-ui, *Chasmistes cujus* Cope, in Pyramid Lake, Nevada: a review. 45:571-603.
Simons, Dwight D. *See* Schulz, Peter D. 33:221-224.
Simpson, Floyd. *See* Baugh, Thomas M. 42:77-80.
Sites, Jack W., Jr. *See* Dobson, Martin L. 47:551-561.
______. *See* Glenn, James L. 50:1-8.
______. *See* Thompson, Pamela 46:224-227.
Skau, C. M. *See* Hixson, S. E. 48:558-562.
Skinner, William D. Size selection of food by cutthroat trout, *Salmo clarki*, in an Idaho stream. 45:327-331.
Skougard, M. *See* Brotherson, J. D. 38:19-30.
Skougard, Michael G. and Jack D. Brotherson. Vegetational response to three environmental gradients in the salt playa near Goshen, Utah County, Utah. 39:44-58.
Skousen, J., J. N. Davis, and Jack D. Brotherson. Comparison of vegetation patterns resulting from bulldozing and two-way chaining on a Utah pinyon-juniper big game range. 46:508-512.
Skousen, Jeffrey G. and Jack D. Brotherson. Behavior and habitat preferences of Ring-necked Pheasants during late winter in central Utah. 42:562-566.
Slagle, R. L. *See* Schowalter, T. D. 48:327-333.
Slaugh, Bartel T., Jerran T. Flinders, Jay A. Roberson, and N. Paul Johnston. Effect of backpack radio transmitter attachment on Chukar mating. 50:379-380.
______, Jerran T. Flinders, Jay A. Roberson, M. Ray Olson, and N. Paul Johnston. Radio transmitter attachment for Chukars. 49:632-636.
Slauson, William L. *See* Welden, Charles W. 50:313-319.
Smith, B. N. *See* Davis, Tim D. 45:520-526.
Smith, Bruce N. *See* Morden, C. 46:140-147.
Smith, Charles Clinton. *See* Bragg, Arthur N. 3:33-50.
Smith, David R. Two pronghorn antelope found locked together during the rut in west central Utah. 50:287.
Smith, Donald D., Philip A. Medica, and Sherburn R. Sanborn. Ecological comparison of sympatric populations of sand lizards (*Cophosaurus texanus* and *Callisaurus draconoides*). 47:175-185.
Smith, Dwight G. Breeding range expansion of the Starling in Utah. 35:419-424.
______ and Joseph R. Murphy. Nest site selection in raptor communities of the eastern Great Basin desert. 42:395-404.
______ and Charles R. Wilson. Notes on the winter food of Screech Owls in central Utah. 31:83-84.
______, Charles R. Wilson, and Herbert H. Frost. Seasonal food habits of Barn Owls in Utah. 32:229-234.
______. *See* Ellis, David H. 29:165-167.
Smith, Frank J. and Elizabeth C. Neese. A new perennial species of *Gilia* (Polemoniaceae) from Utah. 49:461-465.
______. *See* Welsh, Stanley L. 43:371-372.
Smith, Geoffrey V. *See* Ottley, John R. 40:59-62.
Smith, Graham W. Home range and activity patterns of black-tailed jackrabbits. 50:249-256.
______. *See* Wywialowski, Alice P. 48:216-223.
Smith, H. D. *See* Nichols, D. W. 35:191-202.
______. *See* Pritchett, C. L. 47:231-233.
Smith, H. Duane, Mark C. Oveson, and Clyde L. Pritchett. Characteristics of mule deer beds. 46:542-546.
______, Gary H. Richins, and Clive D. Jorgensen. Growth of *Dipodomys ordii* (Rodentia: Heteromyidae). 38:215-221.
______. *See* Belk, Mark C. 50:387-389.
______. *See* Jorgensen, Clive D. 40:282-286.
______. *See* King, Michael M. 40:273-281.
______. *See* Landeen, Dan S. 39:267-273.

______. *See* Mower, Kerry J. 49:552-555.

______. *See* Richins, Gary H. 34:105-120.

______. *See* Robey, Edward H., Jr. 47:488-496.

______. *See* Scrivner, Jerry H. 41:362-367.

Smith, Hobart M. Additions to the knowledge of the herpetofauna of Oaxaca, Mexico. 31:138-139.

______. Rozella Pearl Beverly Blood Smith, 1911-1987. 48:180-187.

______. The snake genus *Amastridium* in Oaxaca, Mexico. 31:254-255.

______. The Sonoran subspecies of the lizard *Ctenosaura hemilopha*. 32:104-111.

______ and William P. Hall. Contributions to the concepts of reproductive cycles and the systematics of the *scalaris* group of the lizard genus *Sceloporus*. 34:97-104.

______ and Kenneth R. Larsen. The generic name of the North American musk turtles. 34:42-44.

______ and Kenneth R. Larsen. The name of the Baja California Cape wormsnake. 34:94-96.

______ and Kenneth R. Larsen. The nominal snake genera *Mastigodryas* Amaral, 1934, and *Dryadophis* Stuart, 1939. 33:276.

______, Rozella B. Smith, and Jean Guibé. The identity of Bocourt's lizard *Eumeces capito* 1879. 35:109-112.

______, Rosella B. Smith, and H. Lewis Sawin. The authorship and date of publication of *Siren intermedia* (Amphibia: Caudata). 35:100-102.

______. *See* Dasmann, Marlene M. 34:231-237.

______. *See* Fawcett, James D. 31:135-137; 31:261-264.

______. *See* Feuer, Robert C. 32:55-60.

______. *See* Pérez-Higareda, Gonzalo 48:263-266.

______. *See* Waddick, James W. 34:257-266.

Smith, J. Steven. *See* Springer, Joseph Tucker 41:449-456.

Smith, L. M. *See* Haukos, D. A. 49:624-626.

Smith, Loren M. and John A. Kadlec. Comparisons of prescribed burning and cutting of Utah marsh plants. 45:462-466.

______. *See* Hupp, Jerry W. 48:202-205.

Smith, Margaret F. *See* Patton, James L. 44:431-440.

Smith, Marion R. Two new ants from western Nevada (Hymenoptera, Formicidae). 11:91-96.

______. Two new species of *Aphaenogaster* (Hymenoptera: Formicidae). 2:118-121.

Smith, Nathan M. Observation of voice in the western collared lizard, *Crotaphytus collaris bicinctores*. 34:276.

______ and Wilmer W. Tanner. Two new subspecies of *Crotaphytus* (Sauria: Iguanidae). 32:25-34.

Smith, Robert L. and Eugene F. Olsen. Sexual imprinting of a Barn Owl (*Tyto alba*) on humans. 36:385-386.

Smith, Rosella B. *See* Smith, Hobart M. 35:100-102; 35:109-112.

Smith, Stuart D., Stephen C. Bunting, and M. Hironaka. Evaluation of the improvement in sensitivity of nested frequency plots to vegetational change by summation. 47:299-307.

Smolik, J. *See* Weaver, T. 47:473-479.

Sneva, Forrest A. *See* Britton, Carlton M. 50:115-120.

Socha, David G. *See* Clark, Tim W. 42:572-582.

Somma, Louis A. Influence of substrate water content on neonate size in the prairie skink, *Eumeces septentrionalis*. 49:198-200.

______. Maternal care of neonates in the prairie skink, *Eumeces septentrionalis*. 47:536-537.

______. Reproduction of the prairie skink, *Eumeces septentrionalis*, in Nebraska. 47:373-374.

______ and Philip A. Cochran. Bibliography and subject index of the prairie skink, *Eumeces septentrionalis* (Baird) (Sauria: Scincidae). 49:525-534.

Sooter, Clarence A. *See* Cottom, Clarence 3:51-53.

Soreng, Robert J. *Poa* L. in New Mexico, with a key to middle and southern Rocky Mountain species (Poaceae). 45:395-422.

Sorensen, Darwin L. *See* Rushforth, Samuel R. 48:324-326.

Sorenson, Edward B. and Robert C. Stones. Description of a new tenebrionid (Coleoptera) from Glen Canyon, Utah. 19:63-66.

Spaulding, Jeanine L. *See* Elliott-Fisk, Deborah L. 43:377-384.

Spence, John R. Checklist of the mosses of Grand Teton National Park and Teton County, Wyoming. 45:124-126.

______. Checklist of the mosses of the Intermountain West, USA. 48:394-401.

______. *Pseudocrossidium aureum* (Bartr.) Zand. (Pottiaceae, Musci) new to Utah. 47:347-348.

______ and Richard J. Shaw. A checklist of the alpine vascular flora of the Teton Range, Wyoming, with notes on biology and habitat preferences. 41:232-242.

______ and Richard J. Shaw. Observations on alpine vegetation near Schoolroom Glacier, Teton Range, Wyoming. 43:483-491.

Springer, Joseph Tucker and J. Steven Smith. Summer food habits of coyotes in central Wyoming. 41:449-456.

Squires, Lorin E., Mark C. Whiting, Jack D. Brotherson, and Samuel R. Rushforth. Competitive displacement as a factor influencing phytoplankton distribution in Utah Lake, Utah. 39:245-252.

______. *See* Rushforth, Samuel R. 45:237-254; 46:398-403.

______. *See* St. Clair, Larry L. 38:211-214.

St. Clair, Larry L., Samuel R. Rushforth, and James V. Allen. Diatoms of Oregon Caves National Monument, Oregon. 41:317-332.

______, Lorin E. Squires, and Samuel R. Rushforth. A comparative analysis of the diatom flora on the snail *Ampullaria cuprina* from the Goshen Ponds, Utah. 38:211-214.

______. *See* Grimes, Judith A. 40:223-228.

______. *See* Johansen, Jeffrey R. 46:632-640.

St. Louis, Martin. *See* Crawford, John A. 46:745-748.
Stackhouse, Mark. *See* Tepedino, Vincent J. 47:314-318.
Stafford, Michael. *See* Youtie, Berta A. 47:644-651.
Stafford, Michael P., William F. Barr, and James B. Johnson. Coleoptera of the Idaho National Engineering Laboratory: an annotated checklist. 46:287-293.
Stafford, S. G. *See* Schowalter, T. D. 48:327-333.
Stanton, N. L. *See* Tepedino, V. J. 40:197-215.
Stanton, Nancy L. *See* Shults, Larry M. 47:103-104; 50:327-331.
Stark, B. P., S. W. Szczytko, and R. W. Baumann. North American stoneflies (Plecoptera): systematics, distribution, and taxonomic references. 46:383-397.
Stark, Bill P. A review of the genus *Soliperla* (Plecoptera: Peltoperlidae). 43:30-44.
______ and Richard W. Baumann. New species of Nearctic *Neoperla* (Plecoptera: Perlidae), with notes on the genus. 38:97-114.
______ and Arden R. Gaufin. The species of *Calineuria* and *Doroneuria* (Plecoptera: Perlidae). 34:83-93.
______, Theodore A. Wolff, and Arden R. Gaufin. New records of stoneflies (Plecoptera) from New Mexico. 35:97-99.
______. *See* Baumann, Richard W. 40:63-67.
______. *See* Cather, Mary R. 35:49-50.
______. *See* Stewart, Kenneth W. 36:366-384; 44:373-415.
Stark, Harold E. Review of tularemia in Utah and the Great Basin. 39:103-121.
______. *See* Tipton, Vernon J. 39:351-418.
Stauffer, Dean F. and Steven R. Peterson. Seasonal microhabitat relationships of Blue Grouse in southeastern Idaho. 46:117-122.
Stebbins, Robert C. *See* Mullen, David A. 38:429-437.
Steele, Benjamin B. and Stephen B. Vander Wall. Aquatic birds of the White River, Uintah County, Utah. 45:113-116.
Steigers, William D., Jr., Jerran T. Flinders, and Susan M. White. Rhythm of fecal production and protein content for black-tailed jackrabbits. 42:567-571.
Stein, Steven J. Fire history of the Paunsaugunt Plateau in southern Utah. 48:58-63.
Stephens, Daniel A. and Timothy D. Reynolds. Birds of southwestern Idaho. 43:728-738.
Stephens, Doyle W. A summary of biological investigations concerning the Great Salt Lake, Utah (1861-1973). 34:221-229.
Stephens, Trent D. *See* Reynolds, Timothy D. 44:166-169.
Stephenson, Stephen N. Mammals of the Paunsagunt Plateau Region, Utah. 26:43-44.
Stern, Mark A. *See* Williams, Jack E. 50:243-248.
Stevens, Richard, Kent R. Jorgensen, and James N. Davis. Viability of seed from thirty-two shrub and forb species through fifteen years of warehouse storage. 41:274-277.
Stewart, David A., Gary M. Booth, and Jerold L. Petty. Emergence data and artificial rearing media for an aspen bark beetle, *Trypophloeus populi* (Coleoptera: Scolytidae). 39:129-132.
Stewart, Kenneth W. and Bill P. Stark. Nymphs of North American Perlodinae genera (Plecoptera: Perlodidae). 44:373-415.
______, Bill P. Stark, and Thomas G. Higgins. The stoneflies (Plecoptera) of Louisiana. 36:366-384.
______. *See* Oberndorfer, Reed Y. 37:260-273.
______. *See* Szczytko, Stanley W. 36:211-220.
______. *See* Todd, C. Stan 45:721-733.
Stewart, Sarah Ann and D. J. Weber. Environmental site characteristics and incidence of chokecherry black knot in Utah. 44:579-583.
Stinson, Nathaniel, Jr. Home range of the western jumping mouse, *Zapus princeps*, in the Colorado Rocky Mountains. 37:87-90.
Stirling, Gray. *See* Collins, Nicholas C. 40:131-138.
Stiver, San J. *See* Goodrich, John M. 49:390-391.
Stockhouse, Robert E., II. Nectar composition of hawkmoth-visited species of *Oenothera* (Onagraceae). 35:273-274.
Stokes, W. L. *See* Thayne, G. F. 43:394-402.
Stones, Robert C. *See* Sorenson, Edward B. 19:63-66.
Stopher, Carol E. *See* Gut, Larry J. 37:523-529.
Storm, Robert M. and Richard A. Pimentel. Herpetological notes from Malheur County, Oregon. 9:59-63.
______. *See* Black, Jeffrey Howard 30:9-12.
______. *See* Ferguson, Denzel E. 18:63-65.
______. *See* Whitaker, John O., Jr. 46:228-240.
Strachan, Jeffrey L. and James L. Reveal. On the typification of *Salvia dorrii* (Lamiaceae). 41:198-200.
Straight, Richard C. *See* Glenn, James L. 50:1-8.
Stromberg, Juliet C. and Duncan T. Patten. Seed production and seedling establishment of a Southwest riparian tree, Arizona walnut (*Juglans major*). 50:47-56.
Stuenkel, Edward L. *See* Deacon, James E. 47:538-546.
Sturges, David L. Soil water withdrawal and root distribution under grubbed, sprayed, and undisturbed big sagebrush vegetation. 40:157-164.
Styler, Eloise L. *See* Reveal, James L. 33:19-25.
Sugden, Evan A. Pollinators of *Astragalus monoensis* Barneby (Fabaceae): new host records; potential impact of sheep grazing. 45:299-312.
Sullivan, Brian K. Advertisement call variation in the Arizona tree frog, *Hyla wrightorum* Taylor, 1938. 46:378-381.
______. Natural hybrid between the Great Plains toad (*Bufo cognatus*) and the red-spotted toad (*Bufo punctatus*) from central Arizona. 50:371-372.
______. Sexual selection and mating system variation in anuran amphibians of the Arizona-Sonoran Desert. 45:688-696.
Surdick, Rebecca F. New Nearctic Chloroperlidae (Plecoptera). 41:349-359.
Sweeney, Steven J. *See* Knick, Steven T. 44:70-74.

Swegman, Bernard G. and Leonard C. Ferrington, Jr. New records of western Trichoptera with notes on their biology. 40:287-291.

Szczytko, S. W. *See* Stark, B. P. 46:383-397.

Szczytko, Stanley W. and Kenneth W. Stewart. Three new species of Nearctic Isoperla (Plecoptera). 36:211-220.

Szyska, Lee A. *See* Brotherson, Jack D. 40:229-253; 41:298-309.

T

Talbot, Stephen S., Sandra J. Looman, and Stanley L. Welsh. *Cicuta bulbifera* L. (Umbelliferae) in Alaska. 48:382.

Tanner, Annie Atkin. "I Do," included a zoo. 30:190-194.

Tanner, Vasco M. American Association for the Advancement of Science. 3:4.

______. Amphibians and reptiles contributed to Brigham Young University by Owen Bryant. 9:47-49.

______. Angus Munn Woodbury, 1886-1964. 25:81-88.

______. Antarctic birds contributed by Dr. Russell G. Frazier. 2:122-124.

______. A biotic study of the Kaiparowits Region of Utah. 1:97-126.

______. Book notice. Taxonomic review: Miridae of the Nevada Test Site and the western United States. 28:47-48.

______. Carl Linnaeus' contributions and collections. 19:27-35.

______. A chapter on the natural history of the Great Basin, 1800 to 1855. 1:33-61.

______. A check-list of the species of *Eleodes* and descriptions of new species (Coleoptera-Tenebrionidae). 21:55-78.

______. Clarence Cottam, 1899-1974: a distinguished alumnus of Brigham Young University. 35:231-239.

______. A comprehensive index to the *Great Basin Naturalist*, volumes 1-30 inclusive, 1939-1970. 31:1-34.

______. D Elden Beck (1906-1967). 27:230-239.

______. Description of new species of *Miloderes* Casey, with comments on other species in the genus (Coleoptera: Curculionidae). 34:291-296.

______. Dr. Henry Clinton Fall (1862-1939). 1:62.

______. Dr. Pfouts contributes butterflies. 1:61.

______. Dr. William Williams Henderson (1879-1944). 5:23-24.

______. Edwin Cooper Van Dyke (1869-1952). 13:29-34.

______. The European earwig found in Provo, Utah. 5:22.

______. European journals and the war. 1:92.

______. The flying squirrel collected in Garfield County, Utah. 1:126.

______. Frank Ellsworth Blaisdell, Sr. (1862-1946). 7:17-20.

______. George Paul Engelhardt (1871-1942). 3:57-58.

______. Gull banding at Utah Lake, No. 3. 8:37-39.

______. Gull banding notes at Utah Lake. 2:98.

______. Interesting Coleoptera records for Utah. 2:36.

______. John E. Blazzard contributes mammal collection. 1:146.

______. Joseph Richard Slevin (1881-1957). 17:56-58.

______. Lesser Yellow Legs, new record for Washington County, Utah. 2:86.

______. Life history notes on *Calligrapha multipunctata multipunctata* (Say) (Coleoptera, Chrysomelidae). 18:101-103.

______. List of insect type specimens in the entomological collection of Brigham Young University, Provo, Utah, No. V. 34:317-322.

______. Margaret Hamilton Storey (1900-1960). 20:70.

______. The Mexican bean beetle, *Epilachna varivestis* Mulsant, does damage in Utah in 1943. 4:61.

______. The Mexican bean beetle taken at Provo, Utah. 1:91.

______. Necrology report of the Department of Zoology and Entomology Alumni, Brigham Young University, 1955. 15:50-54.

______. New bird records from Zion National Park. 2:121-122.

______. New cover design. 14:38.

______. A new *Elaphrus* (Coleoptera, Carabidae). 2:137-138.

______. A new species of *Araeoschizus* (Coleoptera-Tenebrionidae). 6:125-126.

______. A new species of *Craniotus* (Coleoptera: Tenebrionidae). 23:167-170.

______. A new species of *Gila* from Nevada (Cyprinidae). 10:31-36.

______. Notes on some Cicindelidae of the western United States and the South Pacific Islands with a description of a new species. 11:47-51.

______. Notes on the birth and growth of horned lizards. 3:60.

______. Notes on the Gordiacea of Utah. 1:2.

______. Notes on the number, length, and weight of young garter snakes. 9:51-54.

______. Notes on American *Sitona* (Coleoptera: Curculionidae), with three new species. 47:168-174.

______. Onion maggot in Provo area. 20:48.

______. An outbreak of Say's plant bug in Utah Valley, 1958. 18:30.

______. Pacific Islands herpetology, No. I: Mariana Islands: a new species of *Typhlops*. 9:1-20.

______. Pacific Islands herpetology No. II: Philippine Islands. 9:25-39.

______. Pacific Islands herpetology, No. III: Morotai Island. 10:1-30.

______. Pacific Islands herpetology, No. IV: Admiralty Islands. 11:1-10.

______. Pacific Islands herpetology, No. V: Guadalcanal, Solomon Islands: a check list of species. 11:53-86.

______. Pacific Islands herpetology No. VI: Tahiti and Marquesas Islands, New Guinea and Australia. 12:1-12.

______. Pacific Islands herpetology No. VII: Ulu Langat, State of Selangor, Malay. 13:1-7.

______. Pacific Islands herpetology, No. VIII: Korea. 13:67-73.

______. Painted lady butterfly in migration. 2:104.

______. *Ranatra quadridentata* Stal (Nepidae) found in Utah. 7:29.

______. A review of the genus *Notolepidomyzon* with a description of a new species (Pisces-Catostomidae). 3:27-32.

______. Sage Hens killed on highway. 7:30.

______. Sheldon P. Hayes collects cold-blooded vertebrates in Arizona. 3:59.

______. Sir Guy Marshall (1871-1958). 20:78.

______. Small clam attacks young trout. 14:23-25.

______. *Spongilla fragilis* found in Utah Lake and Salem Pond. 1:61.

______. Strawberries damaged by a diplopod. 9:23.

______. Studies in the weevils of western United States, No. III: New species from Utah. 1:31-32.

______. Studies in the weevils of the western United States, No. IV: A new species of *Cimbocera*. 2:29-32.

______. Studies in the weevils of the western United States, No. V: A new species of *Miloderoides*. 3:23-26.

______. Studies in the weevils of the western United States, No. VII: Description of a new genus. 10:71-74.

______. Studies in the weevils of the western United States, No. VIII: Description of new species. 14:73-78.

______. Studies in the weevils of the western United States, No. IX: Description of a new species of *Eucyllus* (Coleoptera: Curculionidae). 19:53-55.

______. A study of the genus *Scaphiopus*: the spade-foot toads. 1:3-26.

______. A study of the subtribe Hydronomi with a description of new species (Curculionidae), study No. VI. 4:1-38.

______. Tortoise-shell butterfly in migration. 13:8.

______. Two new species of weevils of the tribe Celeuthetini (Coleoptera). 20:23-28.

______. White-lined sphinx moth abundant in central Utah, spring 1949. 9:76.

______. Willis Stanley Blatchley (1859-1940). 2:33-35.

______ and D Elden Beck. Gull banding notes at Utah Lake, No. 2. 3:55-57.

______ and Don R. Harris. List of the insect type specimens in the entomological collection of the Brigham Young University, Provo, Utah, No. III. 29:150-164.

______ and Don R. Harris. List of insect type specimens in the entomological collection of the Brigham Young University, Provo, Utah, No. IV. 29:183-205.

______ and Gerald L. Nielsen. *Gastroidea cyanea* Melsh (Coleoptera) preyed upon by an hemipteran predator. 14:27-29.

______ and Willis Packham. *Pelecyphorus semilaevis* (Horn): (Coleoptera: Tenebrionidae). 22:110-113.

______ and Wilmer W. Tanner. Additional records of Coleoptera collected at the Nevada Test Site, Mercury, Nevada. 34:218-220.

______ and Wilmer W. Tanner. Notes on *Charina bottae* in Utah: reproduction. 1:27-30.

______. *See* Allred, Donald M. 39:89-96.

______. *See* Brown, Walter C. 9:41-45.

______. *See* Smith, Nathan M. 32:25-34.

Tanner, Wilmer W. Amphibians of western Chihuahua. 49:38-70.

______. A catalogue of the fish, amphibian, and reptile types in the Brigham Young University Museum of Natural History. 30:219-226.

______. *Diadophis regalis regalis* (B. & G.) found in Nevada. 12:63-64.

______. Evolution of the sceloporine lizards (Iguanidae). 35:1-20.

______. Herpetological notes from the Nevada Test Site. 42:219-222.

______. Lizards and turtles of western Chihuahua. 47:383-421.

______. A new genus of plethodontid salamander from Mexico. 10:37-44.

______. A new *Hypsiglena* from Tiburon island, Sonora, Mexico. 41:139-142.

______. New records and distributional notes for reptiles of the Nevada Test Site. 29:31-34.

______. A new *Sceloporus magister* from eastern Utah. 15:32-34.

______. A new skink of the *multivirgatus* group from Chihuahua. 17:111-117.

______. Notes on a collection of amphibians and reptiles from southern Mexico, with a description of a new *Hyla*. 17:52-56.

______. Notes on the herpetological specimens added to the Brigham Young University Vertebrate Collection during 1939. 1:138-146.

______. Notes on the life history of *Eumeces skiltonianus skiltonianus*. 4:81-88.

______. The reptiles and amphibians of Idaho, No. I. 2:87-97.

______. Reptiles and amphibians of Idaho, No. 2. 44:111-112.

______. Snakes of western Chihuahua. 45:615-676.

______. Status of *Spea stagnalis* Cope (1875), *Spea intermontanus* Cope (1889), and a systematic review of *Spea hammondii* Baird (1839) (Amphibia: Anura). 49:503-510.

______. Status of *Thamnophis sirtalis* in Chihuahua, Mexico (Reptilia: Colubridae). 48:499-507.

______. A study of taxonomy and phylogeny of

Lampropeltis pyromelana Cope. 13:47-66.

______. A study of the variation in the less common snakes of Utah. 2:16-28.

______. A taxonomic and ecological study of the western skink (*Eumeces skiltonianus*). 17:59-94.

______. A taxonomic study of the genus *Hypsiglena*. 5:25-92.

______. Two new skinks from Durango, Mexico. 18:57-62.

______. Two new species of *Hypsiglena* from western North America. 4:49-54.

______ and David F. Avery. Buccal floor of reptiles, a summary. 42:273-349.

______ and Benjamin H. Banta. The distribution of *Tantilla utahensis* Blanchard. 22:116-118.

______ and Benjamin H. Banta. A systematic review of the Great Basin reptiles in the collections of Brigham Young University and the University of Utah. 26:87-135.

______ and Benjamin H. Banta. The systematics of *Crotaphytus wislizeni*, the leopard lizards. Part I: A redescription of *Crotaphytus wislizeni wislizeni* Baird and Girard, and a description of a new subspecies from the Upper Colorado River Basin. 23:129-148.

______ and Benjamin H. Banta. The systematics of *Crotaphytus wislizeni*, the leopard lizards. Part III: The leopard lizards of the Great Basin and adjoining areas, with a description of a new subspecies from the Lahontan Basin. 37:225-240.

______ and Arden H. Brame, Jr. Description of a new species of salamander from Panama. 21:23-26.

______ and Douglas C. Cox. Reproduction in the snake *Lampropeltis pyromelana*. 41:314-316.

______ and John E. Krogh. Ecology of *Sceloporus magister* at the Nevada Test Site, Nye County, Nevada. 33:133-146.

______ and Charles H. Lowe. Variations in *Thamnophis elegans* with descriptions of a new subspecies. 49:511-516.

______ and John R. Ottley. Reproduction in *Hypsiglena*. 41:310.

______ and W. Gerald Robison, Jr. A collection of herptiles from Urique, Chihuahua. 19:75-82.

______, James R. Dixon, and Herbert S. Harris, Jr. A new subspecies of *Crotalus lepidus* from western Mexico. 32:16-24.

______, D. Lowell Fisher, and Thomas J. Willis. Notes on the life history of *Ambystoma tigrinum nebulosum* Hallowell in Utah. 31:213-222.

______. *See* Avery, David F. 30:166-172.

______. *See* Banta, Benjamin H. 24:37-57; 28:183-194.

______. *See* Cox, Douglas C. 37:35-56; 49:482-490.

______. *See* Fanghella, Charles 35:245-268.

______. *See* Grogan, William L., Jr. 34:238-240.

______. *See* Hansen, Afton M. 18:85-100.

______. *See* Larsen, Kenneth R. 34:1-41.

______. *See* Morris, Ronald L. 29:45-81.

______. *See* Ottley, John R. 38:406-410.

______. *See* Pack, Lloyd E., Jr. 30:71-90.

______. *See* Pearce, Richard C. 33:1-18.

______. *See* Tanner, V. M. 1:27-30.

______. *See* Tanner, Vasco M. 34:218-220.

Tanner-White, Merle. *See* White, Clayton M. 45:150-151; 48:64-67.

Tausch, R. J. and P. T. Tueller. Foliage biomass and cover relationships between tree- and shrub-dominated communities in pinyon-juniper woodlands. 50:121-134.

Tausch, Robin J. Comparison of regression methods for biomass estimation of sagebrush and bunchgrass. 49:373-380.

______ and Paul T. Tueller. Comparison of regression methods for predicting singleleaf pinyon phytomass. 48:39-45.

Taye, Alan C. Flora of the Stansbury Mountains, Utah. 43:619-646.

Taylor, Daniel M. Notes on Hells Canyon birds. 49:279-287.

______. Turkey vultures decline at a traditional roosting site. 46:305-306.

Taylor, Frances R., Leah A. Gillman, and John W. Pedretti. Impact of cattle on two isolated fish populations in Pahranagat Valley, Nevada. 49:491-495.

Taylor, Stanley K. *Hydrometra martini* found in central Utah. 18:67.

Tepedino, V. J. Bee visitation of *Phlox bryoides* (Polemoniaceae). 39:197-198.

______. Effects of defoliation on reproduction of a toxic range plant, *Zigadenus paniculatus*. 42:524-528.

______. Notes on the reproductive biology of *Zigadenus paniculatus*, a toxic range plant. 41:427-430.

______ and N. L. Stanton. Spatiotemporal variation in phenology and abundance of floral resources on shortgrass prairie. 40:197-215.

Tepedino, Vincent J. and Mark Stackhouse. Bee visitors of sweetvetch, *Hedysarum boreale boreale* (Leguminosae), and their pollen-collecting activities. 47:314-318.

Terry, Richard E. *See* Burns, Steven J. 46:316-320.

Tew, Richard W. *See* Koenig, Ervon R. 31:106-108.

Thayn, G. F. and W. D. Tidwell. Flora of the Lower Cretaceous Cedar Mountain Formation of Utah and Colorado, Part II: *Mesembrioxylon stokesi*. 44:257-262.

______, W. D. Tidwell, and W. L. Stokes. Flora of the Lower Cretaceous Cedar Mountain Formation of Utah and Colorado. Part I: *Paraphyllanthoxylon utahense*. 43:394-402.

Thayn, Gregory F. *See* Tidwell, William D. 32:1-15; 33:61-76; 46:559-566.

Theodor, O. and B. V. Peterson. On some new species of Nycteribiidae (Diptera: Pupipara). 24:107-115.

Thomas, M. K. *See* Nambudiri, E. M. V. 34:71-81.

Thomas, Rex E. A review of flea collection records from

Onychomys leucogaster with observations on the role of grasshopper mice in the epizoology of wild rodent plague. 48:83-95.

Thompson, H. and B. Prigge. New species and a new combination of *Mentzelia* section *Bartonia* (Loasaceae) from the Colorado Plateau. 46:549-554.

Thompson, Pamela and Jack W. Sites, Jr. Two aberrant karyotypes in the sagebrush lizard (*Sceloporus graciosus*): triploidy and a "supernumerary" oddity. 46:224-227.

Thompson, Steven P. *See* Littlefield, Carroll D. 41:440-444.

Thomson, Robert D. *See* Mahood, Albert D. 44:83-98.

Thorne, Gerald. Some nematodes of the family *Tylenchidae* which do not possess a valvular median esophageal bulb. 2:37-85.

Thorne, K. H. *See* Welsh, S. L. 41:1-108.

Thorne, Kaye H. and Larry C. Higgins. A new species of *Cryptantha* (Boraginaceae) from Nevada. 42:196-198.

______. New variety of *Mentzelia multicaulis* (Loasaceae) from the Book Cliffs of Utah. 46:555-556.

______. New variety of *Mentzelia pumila* (Loasaceae) from Utah. 46:557-558.

______. *See* Welsh, Stanley L. 37:103-104.

Thorne, Kaye Hugie. *See* Welsh, Stanley L. 45:553-555.

Thurow, Thomas L. An ecological and taxonomic investigation of *Peromyscus maniculatus serratus* in Idaho. 38:469-472.

Tibbetts, Ted. A new species in the genus *Neoteneriffiola* from Utah (Acarina: Anystoidea: Teneriffiidae). 18:43-45.

______. Two new laelaptid snake mites from Korea (Acarina: Laelaptidae). 14:67-72.

Tidwell, W. D. *See* Nambudiri, E. M. V. 41:161-166.

______. *See* Thayn, G. F. 43:394-402; 44:257-262.

Tidwell, William D. and Gregory F. Thayn. *Agathoxylon lemonii* sp. nov., from the Dakota Formation, Utah. 46:559-566.

______, David A. Medlyn, and Gregory F. Thayn. Fossil palm materials from the Tertiary Dipping Vat Formation of central Utah. 32:1-15.

______, David A. Medlyn, and Gregory F. Thayn. Three new species of Palmoxylon from the Eocene Green River Formation, Wyoming. 33:61-76.

______. *See* Medlyn, David A. 46:452-458.

______. *See* Nambudiri, E. M. V. 37:241-246; 47:527-535.

Tiedemann, Arthur R. Shrub research consortium formed. 44:182.

Tiernan, Charles F. *See* McArthur, E. Durant 39:81-87.

Tietjen, Howard. *See* Martin, Stephen J. 44:447-449.

Tietjen, Howard P. *See* LaVoie, G. Keith 31:181.

Tinkham, Ernest R. Nearctic desert Decticidae (Orthoptera). Part I: A new genus from California. 32:176-179.

______. Nearctic desert Decticidae (Orthoptera), Part II: A new genus and species from Arizona. 33:43-50.

______. Nearctic desert Decticidae (Orthoptera), Part III: The true tympanum in certain genera with key. 33:197-201.

______. Nearctic desert sand dune Orthoptera. Part XIV: A new *Eremopedes* (Decticidae). 32:223-228.

______. Notes on *Coniana snowi*, an acridid new to the Utah list. 18:66-67.

______. Orthoptera studies in Nearctic desert sand dunes, Part IV: A new *Trimerotropis* from the dunes of eastern New Mexico. 21:51-54.

______. Studies in desert sand dune Orthoptera, Part I: A new species of *Plagiostira* from eastern New Mexico with key and notes. 20:39-47.

______. Studies in Nearctic desert sand dune Orthoptera, Part II: Two new grasshoppers of the genus *Trimerotropis* from the Utah deserts. 20:49-58.

______. Studies in Nearctic desert sand dune Orthoptera, Part III: A new species of *Cibolacris* from northern Chihuahua, Mexico. 21:29-33.

______. Studies in Nearctic desert sand dune Orthoptera, Part V: A new genus and two new species of giant sand treader camel crickets with keys and notes. 22:12-29.

______. Studies in Nearctic desert sand dune Orthoptera, Part VII: A new dwarf race of *Plagiostira gillettei* from a Utah dune, with generic key. 22:105-107.

______. Studies in Nearctic desert sand dune Orthoptera, Part VIII: A grasshopper new to the Utah list. 22:108-109.

______. Studies in Nearctic desert sand dune Orthoptera, Part IX: A new *Trimerotropis* from southern Idaho Dunes. 24:31-35.

______. Studies in Nearctic desert sand dune Orthoptera, Part X: A new genus and species of Stenopelmatine crickets from the Kelso Dunes with notes on its multi-annual life history and key. 25:63-72.

______. Studies in Nearctic desert sand dune Orthoptera, Part XI: A new arenicolous species of *Stenopelmatus* from Coachella Valley with key and biological notes. 28:124-131.

______. Studies in Nearctic desert sand dune Orthoptera, Part XII: A remarkable new genus and species of stenopelmatine crickets from the Viscaino Desert, Baja California, Mexico, with key. 30:173-179.

______. Studies in Nearctic desert sand dune Orthoptera, Part XIII: A remarkable new genus and species of giant black sand treader camel cricket from the San Rafael Desert with key and notes. 30:242-249.

______. Studies in Nearctic desert sand dune Orthoptera. Part XV: Eremogeography of *Spaniacris* with bioecological notes. 35:113-120.

______. Studies in Nearctic desert and sand dune Orthoptera, Part XVI: A new black *Stenopelmatus* from the Mescalero sands. 39:226-230.

______, Clark R. Mahrdt, and Benjamin H. Banta. Notes on *Viscainopelmatus davewerneri* (Orthoptera:

Gryllacrididae, Stenopelmatinae) from the Viscaino Desert, Baja California Sur, Mexico. 34:203-206.

Tipton, V. J. *See* Barnes, A. M. 37:138-206.

Tipton, Vernon J. New distributional records for Utah Siphonaptera. 10:62-65.

______ and Dorald M. Allred. New distribution records of Utah Siphonaptera with the description of a new species of *Megarthroglossus* Jordan and Rothschild 1915. 11:105-114.

______, Harold E. Stark, and John A. Wildie. Anomiopsyllinae (Siphonaptera: Hystrichopsyllidae), II. The genera *Callistopsyllus*, *Conorhinopsylla*, *Megarthroglossus*, and *Stenistomera*. 39:351-418.

______. *See* Herrin, C. Selby 36:113-205.

Titayavan, Manas and Donald W. Davis. Studies of a uniparental form of *Aphytis vandenboschi* (Hymenoptera: Aphelinidae), a parasite of the San Jose scale in northern Utah. 48:388-393.

Todd, C. Stan and Kenneth W. Stewart. Food habits and dietary overlap of nongame insectivorous fishes in Flint Creek, Oklahoma, a western Ozark foothills stream. 45:721-733.

Toft, C. A. and S. L. Welsh. A revision of the *Psoralea lanceolata* complex (Leguminosae). 32:76-87.

Tolle, Duane A. A survey of breeding and migratory birds southwest of Farmington, New Mexico. 37:489-500.

Tourtlotte, Gregory Ira. Studies on the biology and ecology of the northern scorpion, *Paruroctonus boreus* (Girard). 34:167-179.

Toweill, Dale E. and Chris Maser. Food of cougars in the Cascade Range of Oregon. 45:77-80.

Traver, Robbin L. *See* Branham, Joseph M. 35:51-61.

Trumbo, Michael. *See* Hart, E. Blake 43:492-493.

Tuckfield, R. Cary. *See* Pederson, Jordan C. 43:432-437.

Tueller, P. T. *See* Tausch, R. J. 50:121-134.

______. *See* Zamora, B. 33:225-242.

Tueller, Paul T. and Richard E. Eckert, Jr. Big sagebrush (*Artemisia tridentata vaseyana*) and longleaf snowberry (*Symphoricarpos oreophilus*) plant associations in northeastern Nevada. 47:117-131.

______. *See* Tausch, Robin J. 48:39-45.

Tuhy, J. S. *See* Bourgeron, P. S. 50:209-242.

______. *See* Shultz, L. M. 47:287-298.

Turner, David L. *See* Austin, Dennis D. 49:31-35.

Turner, F. B. *See* Hunter, Richard 47:234-238.

Turner, Frederick B. and Roland H. Wauer. A survey of the herpetofauna of the Death Valley area. 23:119-128.

Turner, Monte E. *Drosophila pseudoobscura* (Diptera: Drosophilidae) of the Great Basin IV: A release experiment at Bryce Canyon. 47:32-37.

Tuttle, Donald M. and Edward W. Baker. New records and species of Tetranychidae and Tenuipalpidae (Acarina) from Utah and Idaho. 36:57-64.

Tyus, Harold M. Life strategies in the evolution of the Colorado squawfish (*Ptychocheilus lucius*). 46:656-661.

______ and James M. Beard. *Esox lucius* (Esocidae) and *Stizostendion viterum* (Percidae) in the Green River Basin, Colorado and Utah. 50:33-39.

______ and W. L. Minckley. Migrating Mormon crickets, *Anabrus simplex* (Orthoptera: Tettigoniidae), as food for stream fishes. 48:25-30.

______. *See* Karp, Catherine A. 50:257-264.

U

Ueckert, D. N. *See* Whisenant, S. G. 44:558-562.

Uresk, D. W. *See* Cincotta, R. P. 47:339-343.

Uresk, Daniel W. and Kieth Severson. Waterfowl and shorebird use of surface-mined and livestock water impoundments on the northern Great Plains. 48:353-357.

______ and Jon C. Sharps. Denning habitat and diet of the swift fox in western South Dakota. 46:249-253.

______. *See* Apa, Anthony D. 50:107-113.

______. *See* Deisch, Michele S. 50:347-353.

______. *See* MacCracken, James G. 43:660-668; 45:287-290.

______. *See* Severson, Kieth E. 48:78-82.

______. *See* Sharps, Jon C. 50:339-345.

Urness, Laura A. *See* Olson-Rutz, Kathrin M. 46:217-219.

Urness, P. J. *See* Austin, D. D. 44:572-574.

Urness, Philip J. *See* Austin, Dennis D. 37:101-102; 42:512-516; 47:100-102; 49:31-35.

______. *See* Olson-Rutz, Kathrin M. 46:217-219.

______. *See* Player, Rodney L. 42:517-523.

V

Vale, Thomas R. Invasion of big sagebrush (*Artemisia tridentata*) by white fir (*Abies concolor*) on the southeastern slopes of the Warner Mountains, California. 35:319-324.

Van Cott, John W. A note on *Geranium richardsonii* Fisch. & Trautv. 29:25-27.

Van Dyke, Walt. *See* Crawford, John A. 46:123-127.

Van Dyke, Walter. *See* Crawford, John A. 46:745-748.

Van Epps, Gordon A. *See* Furniss, Malcolm M. 41:290-297.

Vander Wall, Stephen B. *See* Steele, Benjamin B. 45:113-116.

VanLandingham, Sam L. Observations on the ecology and trophic status of Lake Tahoe (Nevada and California, USA) based on the algae from three independent surveys (1965-1985). 47:562-582.

Velazques Solis, Victor M. *See* Ottley, John R. 49:496-502.

Verts, B. J. and Leslie N. Carraway. Dispersal and dispersion of an introduced population of *Sylvilagus floridanus*. 41:167-175.

______. *See* Weiss, Nondor T. 44:563-571.

Vickery, Robert K., Jr. Plasticity and polymorphism in seed germination of *Mimulus guttatus*

(Scrophulariaceae). 43:470-474.
______. Pollination experiments in the *Mimulus cardinalis-M. lewisii* complex. 50:155-159.
______. *See* Hsu, Sun Szen 36:81-85.
______. *See* Hughes, Karen W. 35:240-244.
Vigg, Steven. Species composition and relative abundance of adult fish in Pyramid Lake, Nevada. 41:395-408.
______. Temperature and salinity relationships of the Nevadan relict dace. 42:541-548.
______. Vertical distribution of adult fish in Pyramid Lake, Nevada. 38:417-428.
______ and Thomas J. Hassler. Distribution and relative abundance of fish in Ruth Reservoir, California, in relation to environmental variables. 42:529-540.
______ and Paul A. Kucera. Contributions to the life history of Sacramento perch, *Archoplites interruptus*, in Pyramid Lake, Nevada. 41:278-289.
______. *See* Sigler, William F. 43:1-29; 45:571-603.
Vincent, Frederic. Spawning ecology of the white bass *Roccus chrysops* (Rafinesque) in Utah Lake, Utah. 28:63-69.
Vollmer, A. T., F. Au, and S. A. Bamberg. Observations on the distribution of microorganisms in desert soil. 37:81-86.
Voorhees, Marguerite E. Forage quality of rillscale (*Atriplex suckleyi*) grown on amended bentonite mine spoil. 50:57-62.
Vora, Robin S. A comparison of the spherical densiometer and ocular methods of estimating canopy cover. 48:224-227
______. Potential soil compaction forty years after logging in northeastern California. 48:117-120.
Vucinich, Nancy. Food of larval tui chubs, *Gila bicolor*, in Pyramid Lake, Nevada. 43:175-178.

W

Waddick, James W. and Hobart M. Smith. The significance of scale characters in evaluation of the lizard genera *Gerrhonotus*, *Elgaria*, and *Barisia*. 34:257-266.
Wade, Charles E. *See* Morton, Martin L. 34:121-134.
Wadley, S. R., R. A. Heckmann, R. C. Infanger, and R. W. Mickelsen. Growth of juvenile American lobsters in semiopen and closed culture systems using formulated diets. 42:67-72.
Wagner, M. R. *See* Schmid, J. M. 44:575-578.
Wagner, Michael R. and Robert L. Mathiasen. Dwarf mistletoe-pandora moth interaction and its contribution to ponderosa pine mortality in Arizona. 45:423-426.
______. *See* Blake, Elizabeth A. 46:169-172.
Wagstaff, Fred J. Impact of the 1975 Wallsburg fire on antelope bitterbrush (*Purshia tridentata*). 40:299-302.
Wahle, Bruce M. *See* Bushnell, John H. 47:500-511.
Waite, Sheldon B. A taxonomic revision of *Physaria* (Cruciferae) in Utah. 33:31-36.
Walker, Danny. Sequence of epiphyseal fusion in the Rocky Mountain bighorn sheep. 47:7-12.
Walker, R. F. Ectomycorrhizal formation by *Pisolithus tinctorius* on *Quercus gambelii* x *Quercus turbinella* hybrid in an acidic Sierra Nevada minesoil. 50:367-370.
______. Formation of *Pisolithus tinctorius* ectomycorrhizae on California white fir in an eastern Sierra Nevada minesoil. 50:85-87.
______. *Pisolithus tinctorius*, a Gasteromycete, associated with Jeffery and Sierra lodgepole pine on acid mine spoils in the Sierra Nevada. 49:111-112.
______. *See* Hixson, S. E. 48:558-562.
Wallace, A. *See* Farnsworth, R. B. 36:65-80.
Wallace, Richard L., J. S. Griffith, Jr., D. M. Daley, Patrick J. Connolly, and G. B. Beckham. Distribution of the Shoshone sculpin (*Cottus greenei*: Cottidae) in the Hagerman Valley of south central Idaho. 44:324-326.
______. *See* Diller, Lowell V. 41:154-157.
Walton, T. P. *See* Wambolt, C. L. 50:201-207.
Wambolt, C. L., T. P. Walton, and R. S. White. Sprouting and seedling establishment in plains silver sagebrush (*Artemisia cana* Pursh. ssp. *cana*). 50:201-207.
Wang, Jianguo. *See* Doescher, Paul S. 50:9-19.
Ward, James V. *See* Rader, Russell B. 50:97-106.
Ward, John F. *See* Meehan, William R. 47:22-31.
Ward, John P. and Stanley H. Anderson. Evaluation of wildlife response to a retained mine highwall in south central Wyoming. 49:449-455.
Ward, Richard T. *See* Welden, Charles W. 50:313-319.
Warner, Rose Ella. Description of a new species of *Phyllotrox* infesting seeds of *Acer grandidentatum*, with new synonymy and a note on *Euclyptus* (Coleoptera: Curculionidae: Erirhininae). 36:463-466.
Warnick, Ronald. *See* Lanner, Ronald M. 31:177-180.
Warnock, Robert G. *See* Heckmann, Richard A. 47:355-372.
Warrick, Robert B. SEM analysis of Utah *Equisetum* stems (Equisetaceae). 48:51-57.
Wasbauer, Marius S. The male brachycistidine wasps of the Nevada Test Site (Hymenoptera: Tiphiidae). 33:109-112.
Wasserman, David and Donald J. Nash. Variation in hemoglobin types in the deer mouse (*Peromyscus maniculatus*) along an altitudinal gradient. 39:192-194.
Wauer, Roland H. Scissor-tailed Flycatcher in Death Valley, California. 23:165.
Weaver, T. Climates of fescue grasslands of mountains in the western United States. 39:284-288.
______ and F. Forcella. Biomass of fifty conifer forests and nutrient exports associated with their harvest. 37:395-401.

______ and R. Lund. Diameter-weight relationships for juniper from wet and dry sites. 42:73-76.

______ and J. Smolik. Soil nematodes of northern Rocky Mountain ecosystems: genera and biomasses. 47:473-479.

______. *See* Bourgeron, P. S. 48:301-323.

Webb, G. Merrill and J. D. Brotherson. Time-activity budgets of drake Gadwall and Northern Shovelers on industrial cooling ponds during late winter and early spring in central Utah. 48:280-284.

______ and Jack D. Brotherson. Elevational changes in woody vegetation along three streams in Washington County, Utah. 48:512-529.

______. *See* White, Clayton M. 43:717-727.

Webb, Robert G. and William L. Roueche. Life history aspects of the tiger salamander (*Ambystoma tigrinum mavortium*) in the Chihuahuan Desert. 31:193-212.

Weber, D. J. *See* Bunderson, E. D. 46:427-440.

______. *See* Davis, Tim D. 45:520-526.

______. *See* Hansen, D. J. 35:86-96.

______. *See* Hegerhorst, D. F. 48:1-8.

______. *See* Huang, J. 48:334-347.

______. *See* Khan, M. A. 47:91-95; 47:220-226.

______. *See* Leonard, R. L. 41:377-388.

______. *See* Stewart, Sarah Ann 44:579-583.

Weberg, Phillip S. *See* Anderson, Loran C. 34:151-160.

Weidman, N. *See* Bourgeron, P. S. 48:301-323.

Weiss, Nondor T. and B. J. Verts. Habitat and distribution of pygmy rabbits (*Sylvilagus idahoensis*) in Oregon. 44:563-571.

Welch, Bruce L. and E. Durant McArthur. Wintering mule deer preference for 21 accessions of big sagebrush. 46:281-286.

______ and James N. Davis. In vitro digestibility of *Kochia prostrata* (L.) Schrad. 44:296-298.

______ and Stephen B. Monsen. Winter crude protein among accessions of fourwing saltbush grown in a uniform garden. 41:343-346.

______, Jordan C. Pederson, and Ronald L. Rodriguez. Selection of big sagebrush by Sage Grouse. 48:274-279.

______. *See* Davis, James N. 45:778-783.

______. *See* Jacobson, Tracy L. C. 47:497-499.

______. *See* McArthur, E. Durant 39:81-87.

Welden, Charles W., William L. Slauson, and Richard T. Ward. Spatial pattern and interference in pinyon-juniper woodlands of northwest Colorado. 50:313-319.

Wells, Samuel A. A new *Haliplus* from Warm Springs, Nevada (Coleoptera: Haliplidae). 49:89-91.

Welsh, Blaine T. *See* Chatterley, L. Matthew 42:385-394.

Welsh, S. L., N. D. Atwood, S. Goodrich, E. Neese, K. H. Thorne, and Beverly Albee. Preliminary index of Utah vascular plant names. 41:1-108.

______. *See* Toft, C. A. 32:76-87.

Welsh, Stanley L. A bouquet of daisies (*Erigeron*, Compositae). 43:365-368.

______. Description of a new species of *Dalea* (Leguminosae) from Utah. 31:90-92.

______. Endangered and threatened plants of Utah: a reevaluation. 38:1-18.

______. New and unusual plants from Utah. 30:16-22.

______. New species of *Astragalus* (Leguminosae) from Mesa County, Colorado. 45:31-33.

______. New taxa and combinations in the Utah flora. 46:254-260.

______. New taxa in miscellaneous families from Utah. 46:261-264.

______. New taxa in *Thelesperma* and *Townsendia* (Compositae) from Utah. 43:369-370.

______. New taxa of thistles (*Cirsium*: Asteraceae) in Utah. 42:199-202.

______. Nomenclature changes in the Alaskan flora. 28:147-156.

______. On the distribution of Utah's hanging gardens. 49:1-30.

______. On the typification of *Oxytropis borealis* DC. 50:355-360.

______. *Quercus* (Fagaceae) in the Utah flora. 46:107-111.

______. Revision of the *Phlox austromontana* (Polemoniaceae) complex in Utah. 45:791-792.

______. A species of *Cryptantha* (Boraginaceae) dedicated to the memory of F. Creutzfeldt. 42:203-204.

______. Utah botanical explorer Charles Christopher Parry (28 August 1823 - 20 February 1890). 48:9-18.

______. Utah flora: Cactaceae. 44:52-69.

______. Utah flora: Chenopodiaceae. 44:183-209.

______. Utah flora: Compositae (Asteraceae). 43:179-357.

______. Utah flora: Fabaceae (Leguminosae). 38:225-367.

______. Utah flora: Malvaceae. 40:27-37.

______. Utah flora: miscellaneous families. 40:38-58.

______. Utah flora: Polygonaceae. 44:519-557.

______. Utah flora: Rosaceae. 42:1-44.

______. Utah plant novelties in *Astragalus* and *Yucca*. 34:305-310.

______. Utah plant novelties in *Cymopterus* and *Penstemon*. 35:377-378.

______. Utah plant types--historical perspective 1840 to 1981--annotated list, and bibliography. 42:129-195.

______ and N. Duane Atwood. An undescribed species of *Thelypodiopsis* (Brassicaceae) from the Uinta Basin, Utah. 37:95-96.

______ and L. Matthew Chatterley. Utah's rare plants revisited. 45:173-236.

______ and Sherel Goodrich. A fourth species of *Oreoxis* (Umbelliferae). 45:34-36.

______ and Sherel Goodrich. Miscellaneous plant novelties from Alaska, Nevada, and Utah. 40:78-88.

_____ and Elizabeth Neese. New species of *Hymenoxys* and *Perityle* (Compositae) from Utah. 43:373-374.
_____ and Elizabeth Neese. New variety of *Opuntia basilaris* (Cactaceae) from Utah. 43:700.
_____ and James L. Reveal. Utah flora: Brassicaceae (Cruciferae). 37:279-365.
_____ and Frank J. Smith. New *Haplopappus* variety in Utah (Compositae). 43:371-372.
_____ and Kaye H. Thorne. Plants of Arizona: a new species of *Astragalus* from the Kaibab Plateau. 37:103-104.
_____ and Kaye Hugie Thorne. New *Sclerocactus* (Cactaceae) from Nevada. 45:553-555.
_____, N. Duane Atwood, and Joseph R. Murdock. Kaiparowits flora. 38:125-179.
_____, N. Duane Atwood, and James L. Reveal. Endangered, threatened, extinct, endemic, and rare or restricted Utah vascular plants. 35:327-376.
_____. *See* Atwood, N. Duane 44:263-264; 45:485-487; 48:495-498.
_____. *See* Barneby, Rupert C. 45:551-552.
_____. *See* Chatterley, L. Matthew 42:385-394.
_____. *See* Goodrich, Sherel 43:375.
_____. *See* Heil, Ken 46:677-678.
_____. *See* Heil, Kenneth D. 49:100-103.
_____. *See* Kass, Ronald J. 45:548-550.
_____. *See* Neese, Elizabeth 43:429-431; 45:789-790.
_____. *See* Northstrom, Terry E. 30:109-130.
_____. *See* Talbot, Stephen S. 48:382.
Werschkul, David F. Species-habitat relationships in an Oregon cold desert lizard community. 42:380-384.
West, N. E. *See* Bjerregaard, R. S. 44:327-337.
Westcott, Richard L. *See* Jorgensen, Clive D. 46:173-174.
Westfall, Stanley E. *See* Ratliff, Raymond D. 47:422-426.
Weston, J. Bradford and David E. Ellis. Ground nesting of the Ferruginous Hawk in west-central Utah. 28:111.
Wheeler, George C. and Jeanette Wheeler. Mountain ants of Nevada. 38:379-396.
_____ and Jeanette Wheeler. Nest of *Formica propinqua* (Hymenoptera: Formicidae). 41:389-392.
Wheeler, Jeanette. *See* Wheeler, George C. 38:379-396; 41:389-392.
Whisenant, S. G., C. J. Scifres, and D. N. Ueckert. Soil water and temperature response to prescribed burning. 44:558-562.
Whisenant, Steven G. *See* Zou, Jiping. 49:435-448.
Whitaker, John O., Jr. and Chris Maser. Mites (excluding chiggers) of mammals of Oregon. 45:67-76.
_____, Chris Maser, Robert M. Storm, and Joseph J. Beatty. Food habits of clouded salamanders (*Aneides ferreus*) in Curry County, Oregon (Amphibia: Caudata: Plethodontidae). 46:228-240.
Whitaker, John O. *See* Brown, Barbara A. 46:421-426.
White, Clayton M. and Merle Tanner-White. Unusual social feeding and soaring by the Common Raven (*Corvus corax*). 45:150-151.
_____ and Merle Tanner-White. Use of interstate highway overpasses and billboards for nesting by the Common Raven (*Corvus corax*). 48:64-67.
_____, Herbert H. Frost, Dennis L. Shirley, G. Merrill Webb, and Richard D. Porter. Bird distributional and breeding records for southeastern Idaho, Utah, and adjacent regions. 43:717-727.
_____. *See* Black, Hal L. 28:200.
_____. *See* Emison, William B. 48:533-540.
_____. *See* Grebence, Brandon L. 49:408-418.
_____. *See* Mosher, James A. 38:438-446.
White, David A. The infection of immature aquatic insects by larval *Paragordius* (Nematomorpha). 29:44.
_____. *See* Lewellen, Gale R. 31:169-176.
_____. *See* Winger, Parley V. 32:211-219.
White, R. S. *See* Wambolt, C. L. 50:201-207.
White, Susan M. *See* Steigers, William D. 42:567-571.
Whiting, Mark C., Jack D. Brotherson, and Samuel R. Rushforth. Environmental interaction in summer algal communities of Utah Lake. 38:31-41.
_____. *See* Squires, Lorin E. 39:245-252.
Wigand, Peter Ernest. Diamond Pond, Harney County, Oregon: vegetation history and water table in the eastern Oregon desert. 47:427-458.
Wilcox, Bruce A. *See* Holmes, Jennifer A. 45:483-484.
Wilcox, Richard B. *See* Evenson, William E. 40:167-174.
Wilde, Gene R. Foods and feeding periodicity of the White River springfish, *Crenichthys baileyi*. 49:249-251.
_____ and Larry J. Paulson. Food habits of young-of-year largemouth bass in Lake Mead and Lake Mohave, Arizona-Nevada. 48:485-488.
Wildie, J. A. *See* Barnes, A. M. 37:138-206.
Wildie, John A. *See* Tipton, Vernon J. 39:351-418.
Wilhelm, Dallas E. *See* Finley, Robert B. 43:554-560.
Wilken, D. and J. S. Peterson. Distributional records for the Colorado flora II. 44:516-517.
_____, W. Harmon, C. Feddema, and H. Harrington. Distributional records for the Colorado flora. 38:208-210.
Williams, Cecil S. *See* Cottam, Clarence 3:51-53.
Williams, Cynthia D. *See* Williams, Jack E. 40:101-114.
Williams, Jack E. and Carl E. Bond. Status and life history notes on the native fishes of the Alvord Basin, Oregon and Nevada. 43:409-420.
_____ and James E. Deacon. Subspecific identity of the Amargosa pupfish, *Cyprinodon nevadensis*, from Crystal Spring, Ash Meadows, Nevada. 46:220-223.
_____ and Cynthia D. Williams. Feeding ecology of *Gila boraxobius* (Osteichthyes: Cyprinidae) endemic to a thermal lake in southeastern Oregon. 40:101-114.
_____, Mark A. Stern, Alan V. Munhall, and Gary A. Anderson. Conservation status of threatened fishes in Warner Basin, Oregon. 50:243-248.

Willis, Thomas J. *See* Tanner, Wilmer W. 31:213-222.

Wilson, Charles R. *See* Smith, Dwight G. 31:83-84; 32:229-234.

Wilson, M. V. *See* Jensen, M. E. 48:403-421; 48:422-433.

Wilt, F. Martin, Glenn C. Miller, and Richard L. Everett. Monoterpene concentrations in litter and soil of singleleaf pinyon woodlands of the western Great Basin. 48:228-231.

Winger, Parley V., Edward J. Peters, Michael J. Donahoo, James R. Barnes, and David A. White. A checklist of the macroinvertebrates of the Provo River, Utah. 32:211-219.

Winget, R. N. *See* Henderson, J. M. 44:471-481.

Winget, Robert N. Ecological studies of a regulated stream: Huntington River, Emery County, Utah. 44:231-256.

______. *See* Heckmann, Richard A. 44:75-82.

Winkel, Von. *See* Brotherson, Jack D. 46:535-541.

Winward, Alma H. *See* Goodrich, Sherel 45:99-104.

Wirth, Willis W. *See* Grogan, William L., Jr. 35:275-287.

Woffinden, Neil D. Notes on the Swainson's Hawk in central Utah: insectivory, premigratory aggregations, and kleptoparasitism. 46:302-304.

______ and James A. Mosher. Ground nesting and aggressive behavior by the Swainson's Hawk (*Buteo swainsoni*). 39:253-254.

______ and Joseph R. Murphy. Population dynamics of the Ferruginous Hawk during a prey decline. 37:411-425.

Wolfe, Michael L. *See* Austin, Dennis D. 37:101-102.

Wolff, Theodore A. *See* Stark, Bill P. 35:97-99.

Wood, Alan K. and Jack D. Brotherson. Microenvironment and nest site selection by Ring-necked Pheasants in Utah. 41:457-460.

______ and Jack D. Brotherson. Overwinter survival of Ring-necked Pheasants in Utah. 41:247-250.

Wood, B. W. *See* Leonard, R. L. 41:377-388.

Wood, Benjamin W. *See* Pritchett, Clyde L. 40:303-350.

Wood, Karl. *See* Blackburn, Wilbert H. 50:41-46.

Wood, Stephen L. Bark beetles of the genus *Pityoborus* Blackman (Coleoptera: Scolytidae). 18:46-56.

______. The genus *Eupagiocerus* Blandford (Scolytidae, Coleoptera). 25:31-35.

______. Introduced and exported American Scolytidae (Coleoptera). 37:67-74.

______. A key to species of the *Cnesinus* LeConte (Coleoptera: Scolytidae) of North and Central America. 28:88-110.

______. Miscellaneous taxonomic notes on Scolytidae (Coleoptera). 22:76-82.

______. New American bark beetles (Coleoptera: Scolytidae), with two recently introduced species. 40:353-358.

______. A new *Dactylipalpus* (Coleoptera: Scolytidae) from the Philippine Islands. 21:8-9.

______. New genera and new generic synonymy in Scolytidae (Coleoptera). 40:89-97.

______. A new generic name for and some biological data on an unusual Central American beetle (Coleoptera: Platypodidae). 17:103-104.

______. New generic synonymy and new genera of Scolytidae (Coleoptera). 44:223-230.

______. New *Pseudoxylechinus* (Coleoptera: Scolytidae) from India. 46:468.

______. New records and species of American Platypodidae (Coleoptera). 31:243-253.

______. New records and species of Arizona bark beetles (Coleoptera: Scolytidae). 19:57-62.

______. New records and species of Neotropical bark beetles (Scolytidae: Coleoptera). 27:79-97.

______. New records and species of Neotropical bark beetles (Scolytidae: Coleoptera), Part II. 27:119-141.

______. New records and species of Neotropical bark beetles (Scolytidae: Coleoptera), Part III. 28:1-15.

______. New records and species of Neotropical Platypodidae (Coleoptera). 26:45-70.

______. New records and species of Scolytidae (Coleoptera) from Colombia. 21:1-7.

______. New records and species of Scolytidae (Coleoptera) from western North America. 20: 59-69.

______. New species of American bark beetles (Coleoptera: Scolytidae). 42:223-231.

______. New species of American Corthylini (Coleoptera: Scolytidae). 34:135-150.

______. New species of American *Corthylus* (Coleoptera: Scolytidae). 34:181-202.

______. New species of American *Microcorthylus* (Coleoptera: Scolytidae). 33:265-275.

______. New species of bark beetles (Coleoptera: Scolytidae), mostly Mexican. Part IV. 17:105-110.

______. New species of bark beetles (Coleoptera: Scolytidae), mostly Mexican, Part V. 19:1-7.

______. New species of bark beetles (Coleoptera: Scolytidae), mostly Mexican, Part VI. 21:87-107.

______. New species of bark beetles (Coleoptera: Scolytidae), mostly Mexican. Part VII. 27:36-57.

______. New species of bark beetles (Scolytidae: Coleoptera) from western North America. 31:69-76.

______. New species of North American *Pityophthorus* Eichhoff (Coleoptera: Scolytidae). 24:59-70.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae). 35:21-32.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae). Part II. 35:391-401.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae). Part III. 36:347-365.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part IV. 37:207-220.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae). Part V. 37:383-394.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part VI. 37:511-522.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part VII. 38:397-405.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part VIII. 39:133-142.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part IX. 43:647-659.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae). Part X. 44:113-119.

______. New synonymy and new species of American bark beetles (Coleoptera: Scolytidae), Part XI. 46:265-273.

______. New synonymy and new species of bark beetles (Coleoptera: Scolytidae). 45:266-275.

______. New synonymy and records of American bark beetles (Coleoptera: Scolytidae). 34:277-290.

______. New synonymy and records of Platypodidae and Scolytidae (Coleoptera). 29:113-128.

______. New synonymy in American bark beetles (Scolytidae: Coleoptera). 31:140-152.

______. New synonymy in American bark beetles (Scolytidae: Coleoptera), Part II. 32:190-201.

______. New synonymy in American bark beetles (Scolytidae: Coleoptera), Part III. 33:169-188.

______. New synonymy in the bark beetle tribe Cryphalini (Coleoptera: Scolytidae). 32:40-54.

______. New synonymy in the Platypodidae and Scolytidae (Coleoptera). 26:17-33.

______. Nomenclatural changes and new species in Platypodidae and Scolytidae (Coleptera). 41:121-128.

______. Nomenclatural changes and new species of Scolytidae (Coleoptera). 48:31-38.

______. Nomenclatural changes and new species of Scolytidae (Coleoptera), Part II. 48:188-195.

______. Nomenclatural changes and new species of Scolytidae (Coleoptera), Part III. 48:196-201.

______. Nomenclatural changes and new species of Scolytidae (Coleoptera), Part IV. 49:167-185.

______. On the taxonomic status of Platypodidae and Scolytidae (Coleoptera). 33:77-90.

______. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). 23:1-116.

______. Six new Scolytidae (Coleoptera) from Mexico. 47:547-550.

______. Some virtually unknown North American Platypodidae (Coleoptera). 18:37-40.

______. A wolverine in Utah. 18:56.

______ and Fu-sheng Huang. New genus of Scolytidae (Coleoptera) from Asia. 46:465-467.

______ and Hui-fen Yin. Relict occurrence of three "American" Scolytidae (Coleoptera) in Asia. 46:461-464.

Woolley, Tyler A. A new genus and species of oribatid mite (Acari: Liacaroidea, Metrioppiidae). 29:137-139.

______. A new species of *Gymnodamaeus* from Colorado (Acarina: Cryptostigmata, Gymnodamaeidae). 32:97-103.

______. A new species of *Oppia* from Colorado (Cryptostigmata; Oppiidae). 29:133-136.

______ and Harold G. Higgins. Megeremaeidae, a new family of oribatid mites (Acari: Cryptostigmata). 28:172-175.

______ and Harold G. Higgins. A new genus and species of oribatid from pack rat nests (Acari: Cryptostigmata, Tectocepheidae). 28:144-146.

______ and Harold G. Higgins. A new genus and species of oribatid mite from Colorado (Acari: Oribatei, Ceratoppiidae). 25:59-62.

______ and Harold G. Higgins. A new species of *Sphodrocepheus* from the western U.S. (Acari: Cryptostigmata, Cepheidae). 28:176-178.

______ and Harold G. Higgins. Two new species of *Gymnodamaeus* from Colorado (Acarina: Cryptostigmata, Gymnodamaeidae). 33:37-42.

______. *See* Higgins, Harold G. 22:93-100; 28:44-46; 28:142-143; 28:179-182; 29:140-142; 32:208-210; 35:103-108; 36:496-500.

Workman, Gar W. *See* Sigler, William F. 43:1-29.

Worthen, Gary L. Does *Vireo gilvus swainsonii* occur in Utah? 29:181-182.

______. A record of an Indigo Bunting and a wintering Say's Phoebe for northern Utah. 32:220.

Worthen, S. Dick. *See* Cedarleaf, Joy D. 42:91-95.

Worthington, Richard D. and Edward R. Arvizo. Density, growth, and home range of the lizard *Uta stansburiana stejnegeri* in southern Dona Ana County, New Mexico. 33:124-128.

Worthylake, Kathleen Muriel and Peter Hovingh. Mass mortality of salamanders (*Ambystoma tigrinum*) by bacteria (*Acinetobacter*) in an oligotrophic seepage mountain lake. 49:364-372.

Wray, D. L. and G. F. Knowlton. Additions to the list of the Collembola of Utah. 13:43-46.

______ and G. F. Knowlton. Further additions to the list of Collembola of Utah. 16:7-8.

______ and G. F. Knowlton. A preliminary list of Collembola of Idaho. 16:1-6.

Wullstein, L. H. *See* Neilson, Ronald P. 46:294-298.

Wyckoff, John W. The effects of soil texture on species diversity in an arid grassland of the eastern Great Basin. 33:163-168.

______. Evaluating the relationship between mule deer pellet-group data and available winter range, using LANDSAT imagery. 41:213-220.

Wydoski, Richard S. *See* McAda, Charles W. 45:281-286.

Wywialowski, Alice P. and Graham W. Smith. Selection of microhabitat by the red-backed vole, *Clethrionomys gapperi*. 48:216-223.

Y

Yeaton, Richard I. Ecomorphology and habitat utilization of *Echinocereus engelmannii* and *E. triglochidiatus* (Cactaceae) in southeastern California. 42:353-359.

Yeatts, Loraine. *See* Jennings, William 46:175-177.

Yensen, Dana L. The 1900 invasion of alien plants into southern Idaho. 41:176-183.

Yi, Jea Kim and Richard A. Heckmann. Morphological characteristics of *Dentostomella translucida*, a nematode (Oxyuroidea) found in Mongolian gerbils. 48:206-215.

Yin, Hui-fen. *See* Wood, Stephen L. 46:461-464.

Yochem, Pamela K. *See* Paul, Don S. 50:299-302.

Young, James A., Raymond A. Evans, Bruce A. Roundy, and John A. Brown. Dynamic landforms and plant communities in a pluvial lake basin. 46:1-21.

______. *See* Poole, Stephen C. 49:201-213.

Youtie, Berta A., Michael Stafford, and James B. Johnson. Herbivorous and parasitic insect guilds associated with Great Basin wildrye (*Elymus cinereus*) in southern Idaho. 47:644-651.

Z

Zamora, B. and P. T. Tueller. *Artemisia arbuscula*, *A. longiloba*, and *A. nova* habitat types in northern Nevada. 33:225-242.

Zegers, David A. Time budgets of Wyoming ground squirrels, *Spermophilus elegans*. 41:221-228.

Zentz, W. R. and W. R. Jacobi. Ecology of *Comandra umbellata* (Santalaceae) in western Wyoming. 49:650-655.

Zielinski, W. J. Plague in pine martens and the fleas associated with its occurrence. 44:170-175.

Zimmerman, G. Thomas and Richard D. Laven. Effects of forest fuel smoke on dwarf mistletoe seed germination. 47:652-659.

Zolnerowich, G. *See* Seiler, G. J. 47:280-282.

Zou, Jiping, Jerran T. Flinders, Hal L. Black, and Steven G. Whisenant. Influence of experimental habitat manipulation on a desert rodent population in southern Utah. 49:435-448.

Zug, G. R. Fossil chelonians, *Chrysemys* and *Clemmys*, from the upper Pliocene of Idaho. 29:82-87.

PART II

SUBJECT INDEX

(To determine the year of publication, add 1940 to volume numbers beginning with volume 10. During World War II publication of the *Great Basin Naturalist* was, of necessity, less structured. Consequently, some early volumes cover more than a year; others are limited to one issue consisting of the four quarterly numbers. Consult a library for accurate publication dates for volumes 1-9.)

A

AAAS, announcement of meeting 3:4
Abatorus allredi 25:39-42
Abdastartus ***longulus*** 13:91-99
Abies concolor
  Growth variation, Central Utah 39:219-225
  Invades *Artemisia tridentata*, California 35:319-324
Abronia
  argillosa 40:78-88
  nana ***harrisii*** 46:254-260
Acacicis
  bicornis 48:31-38
  zeylanicus 48:31-38
Acanthochila
  comentis 13:13-16
  rustica ***plana*** 13:13-16
Acanthotomicus ***ipsimorphus*** 45:266-275
Acari
  Ametroproctus, systematics, United States 28:44-46
  Eupterotegaeus, systematics, Oregon 28:179-182
  Exochocepheus, systematics 28:144-146
  Laelaps
    Systematics, keys, Ethiopian Region 36:113-206
  Megeremaeidae, systematics 28:172-175
  Metapyroppia, systematics 29:137-139
  Microzetes auxiliaris appalachicola
    Systematics 28:142-143
  Oppia ***coloradensis***
    Systematics, Colorado 29:133-136
  Oribatella, systematics 30:5-8
  Paenoppia, systematics, Colorado 25:59-62
  Peloptulus, systematics, Western Colorado 32:208-210
      Sphodrocepheus
    Systematics, Western United States 28:176-178
  Systematics, United States 25:55-58
  Trombiculidae
    Systematics, keys, Venezuela 37:501-509
Acarina
  Acomatacarus, systematics, Utah 13:87-90
  Caeculus, systematics, Oregon 17:27-29
  Eremaeus
    Systematics, Western United States 22:89-92
  Gymnodamaeus
    Systematics, Colorado 32:97-103; 33:37-42
  Liacarus ***lectronus***, systematics 29:140-142
  Neoteneriffiola, systematics, Utah 18:43-45
  Ophidilaelaps, systematics, Korea 14:67-72
  Passalozetes, systematics, Utah 22:93-100
  Spinibdella, systematics, Utah 27:98-101
  Suctobelbidae, systematics, Colorado 36:496-500
  Systematics
    Idaho and Utah 36:57-64
    Yampa Valley, Colorado 35:103-108
  Trombicula
    Systematics, Western North America 24:13-17
  Trombiculidae, systematics, keys, Utah 15:1-26
Acer saccharum grandidentatum
  Root system 22:114-115
Acerates decumbens erecta 32:221-222
Acetylene
  Nitrification blockage in soils 46:316-320
  Reduction, mammal feces 46:646-650
Achorutes ***thomomys*** 4:39-48
Acinetobacter
  Mass mortality in *Ambystoma tigrinum* 49:364-372
Acmaeodera ***diffusa*** 29:11-19
Acomatacarus ***sexacis*** 13:87-90
Acrantus ***opimus*** 45:266-275
Afrotingis eumenes 24:83-92
Agathoxylon ***lemonii*** 46:559-566
Agavaceae, *Yucca*, systematics, Utah 45:789-790
Agelena naevia
  Organ Pipe Cactus National Monument, Arizona, microhabitat 45:546-547
Aglais californica, migration, Utah 13:8
Agonistic behavior
  California ground squirrel 48:19-24
Agropyron arizonicum X *Sitanion hystrix brevifolium* X *Agrositanion pinalenoensis*, hybrid from Arizona 43:131-136
Alarm call, *Brachylagus idahoensis* 41:158-160
Alaska
  Amchitka, Aleutian Islands

        - Rock Ptarmigan, foods and weights 48:533-540
    - Anisakid larvae in fishes 45:427-431
- Albinism, *Thomomys talpoides* 31:181
- *Alectoris chukar*
    - Radio transmitter attachment 49:632-636
        - Effect on mating 50:379-380
- Algae
    - Bottle Hollow Reservoir, Utah
        - Checklist, distribution 42:205-218
    - Brigham Young University Campus
        - Checklist 37:402-406
    - Communities, Utah Lake, Utah 38:31-41
    - Lake Tahoe, ecological indicators 47:562-582
    - Navajo National Monument, Arizona 41:433-439
    - Soil
        - Cryptogamic crusts, Uintah Basin, Utah 45:432-442
    - Utah, checklist 48:154-179
    - Utah Lake, Utah
        - Checklist 30:99-105; 31:125-134; 45:237-254
- Allelopathic effects, *Ranunculus testiculatus* 38:90-96
- *Alloperla*
    - ***furcula*** 41:349-359
    - ***hamata*** 41:349-359
    - ***roberti*** 41:349-359
- ***Allozetes harpezus*** 25:55-58
- Alpine plant communities
    - Kings Peak, Uinta Mountains, Utah 42:50-59
- Alvord Basin, Oregon-Nevada
    - Life history of native fishes 43:409-420
- *Alyssum* ***turgidum*** 24:7-12
- *Amastridium*, systematics, Mexico 31:254-255
- *Amblycheila* ***utahensis*** 11:47-51; 20:79-80
- ***Ambotingis*** (Tingidae) 20:29-38
- *Ambrosia dumosa*
    - Competition between adults and seedlings, Mohave Desert, Nevada 49:79-84
- *Ambrosiodmus*
    - ***ferus*** 46:265-273
    - ***paucus*** 46:265-273
- *Ambrysus* ***scolius*** 30:1-4
- *Ambystoma*
    - Relictual population
        - Grass Lake, California 38:429-437
    - *tigrinum*
        - Idaho distribution 44:313-316; 45:291-292
        - Mass mortality by *Acinetobacter*, Wasatch Mountains, Utah 49:364-372
    - *tigrinum mavortium*
        - Life history, Chihuahuan Desert, New Mexico 31:193-212
    - *tigrinum melanostictum*
        - Feeding habits, Eastern Washington 46:299-301
    - *tigrinum nebulosum*
        - Predation on *Limnephilus* 43:475-476
        - Life history, Mt. Timpanogos, Utah 31:213-222
- American Museum of Natural History
    - Southwestern Research Station 14:91
- ***Ametroproctus oresbios*** 28:44-46
- ***Ammopelmatus kelsoensis*** 25:63-71
- *Ammospermophilus leucurus*
    - North Central Nevada 44:428-430
- Amphibians
    - *Ambystoma*, systematics, California 38:429-437
    - Biogeography, Intermountain Region 46:736-744
    - Chihuahua, Mexico 19:75-82
    - Death Valley, California 23:119-128
    - Idaho
        - Checklist 2:87-97
        - Richard P. Erwin collections 44:111-112
    - Observations, Las Vegas, New Mexico 2:109-117
    - Oklahoma, Greer County 15:27-31
    - *Scaphiopus*, systematics 1:3-25
    - *Spea*, systematics 49:503-510
    - Systematics
        - Southern Mexico 17:52-56
        - Western Chihuahua, Mexico 49:38-70
- *Amphicosmus* ***arizonensis*** 19:67-74
- *Amphicranus*
    - ***argutus*** 36:347-365
    - ***fulgidus*** 36:347-365
    - ***micans*** 36:347-365
    - ***parilis*** 35:21-32
    - ***quercus*** 27:36-57
    - ***rameus*** 27:36-57
    - ***spectus*** 40:353-358
    - ***splendens*** 42:223-231
- *Ampullaria cuprina*
    - Diatom flora on, Goshen Ponds 38:211-214
- *Anabrus simplex*
    - Migrating, food for stream fishes 48:25-30
- ***Anaxyleborus*** (Scolytidae) 40:89-97
- *Androsace alaskana* ***reedae*** 40:78-88
- *Aneides ferreus*, food habits, Oregon 46:228-240
- Anisakid larvae, Alaska and Idaho fishes 45:427-431
- *Anomiopsyllus*
    - *amphibolus* 40:361
    - Systematics, keys 37:138-206
- *Anommatocoris* ***zeteki*** 22:8-11
- *Anopheles*, records and observations, Montana 7:23-28
- Anoplura
    - Great Salt Lake Desert, Utah, keys 16:9-17
    - Systematics, host-parasite list, Panama 32:121-136
- Antelope, pronghorn
    - Antipredatory behavior 43:88-92
    - Fecal pellet similarities to deer 38:222-224
    - Locked together in rut, West Central Utah 50:287
- Antelope Island, Great Salt Lake, Utah
    - Barn Owl diet and mammals 46:307-309
- *Antilocapra*
    - *americana*
        - Fecal pellet similarities to deer 38:222-224
    - *americana americana*
        - Locked together in rut, West Central Utah 50:287
- Ants
    - Ecology
        - Northern Arizona 39:97-102

    - Southern Utah 39:97-102
  - Harvester
    - Cold desert rodent competition 39:267-273
  - Mountain, Nevada, checklist and ecology 38:379-396
  - National Reactor Testing Station, Idaho 31:237-242
  - Predaceous-scavenger, Utah 27:67-78
  - Systematics
    - Keys, distribution, Utah 42:415-511
    - Western Nevada 11:91-96
  - Western harvester
    - Prairie dog diggings in mounds, Utah 49:36-37
    - Swarming 40:165-166
  - Western thatching, flights of, Nevada 32:202-207
- Anura
  - Ecology and natural history
    - Oklahoma 3:33-50; 4:62-80
  - Systematics, keys, Oklahoma 4:62-80
- *Apatemon gracilis*
  - Leech penetration and localization 36:97-100
- *Aphaenogaster*
  - ***boulderensis*** 2:118-121
  - ***floridana*** 2:118-121
- *Aphanarthrum*
  - ***indicum*** 48:188-195
  - ***reticulatum*** 48:188-195
  - ***royaleanum*** 48:188-195
- *Aphanizomenon flos-aquae*
  - Competitive displacement and distribution 39:245-252
- ***Aphanocleptus coniferae*** 20:59-69
- Aphidae
  - *Cinara*, systematics 14:11-13
  - *Cinara puerca*, morphology 14:83-86
- Aphididae, systematics, Colorado 12:57-61
- Aphids
  - Descriptions, Luigi Macchiati 12:55-57
  - Dodder, Logan, Utah 8:36
  - Mt. Timpanogos, Utah, checklist 7:1-6
- *Aphrophora canadensis*
  - Bionomics on mugo pine, Idaho 44:338-348
- *Aphrosylus* ***wirthi*** 11:11-17
- *Aphytis vandenboschi*
  - Uniparental form, Northern Utah 48:388-393
- Apiaceae, systematics, keys, Utah 46:66-106
- ***Apoxyleborus*** (Scolytidae) 40:89-97
- Apple orchards, Utah
  - Phytoseiid predators of mite pests 39:63-80
- Aquaculture
  - Multiple use systems 44:471-481
  - Warm water
    - Waste heat and water from power plants 44:75-82
- *Aquilegia formosa* ***fosteri*** 46:254-260
- *Arabis* ***vivariensis*** 46:261-264
- Arachnids, as ecological indicators 35:405-406
- *Araeoschizus* ***airmeti*** 6:125-126
- *Araptus*
  - ***attenuatus*** 35:21-32
  - ***consobrinus*** 35:391-401
  - ***crassus*** 37:207-220
  - ***fossifrons*** 35:21-32
  - ***gracilens*** 36:347-365
  - ***micaceus*** 35:391-401
  - ***micropilosus*** 42:223-231
  - ***morigerus*** 42:223-231
  - ***obesus*** 37:207-220
  - ***placetulus*** 42:223-231
  - ***sobrinus*** 34:277-290
  - ***speciosus*** 40:353-358
- Aravaipa Creek, Arizona
  - Feeding interrelations of native fishes 41:409-426
- *Arceuthobium*
  - *apachecum* 42:120-127
  - *blumeri* 42:120-127
  - *cyanocarpum*, distribution, Nevada 50:91-92
  - *douglasii*
    - Douglas-fir infection, Southwest 50:67-71
    - Effects on Douglas-fir, Southwest 50:173-179
  - Range extensions, systematics, Southwest 43:741-476
  - Systematics 42:120-127
- *Archoplites interruptus*
  - Life history in Pyramid Lake, Nevada 41:278-289
- *Ardea herodias*
  - Found dead at 11,000 feet, Utah 32:112
- *Arenaria laricifolia* ***hultenii*** 28:147-156
- Argentina, *Nothofagus* forest
  - Fungi in small mammals 49:618-620
- *Argyra* ***utahna*** 11:11-17
- Arid Land Ecology Reserve, Washington
  - *Spermophilus townsendi*, food 37:128
- Arizona
  - Aravaipa Creek
    - Feeding interrelations of native fishes 41:409-426
  - Basidiomycetes that decay junipers 38:42-48
    - Keys 35:288-304
  - Bylas Springs, endangered Sonoran topminnow
    - Management 50:265-273
  - Casa Grande National Monument
    - Mesquite 31:153-159
  - Cold-blooded vertebrate collecting 3:59
  - *Cowania* and its intergeneric hybrids 44:484-486
  - Dwarf mistletoe-pandora moth interaction
    - Ponderosa pine mortality 45:423-426
  - Grand Canyon National Park, cryptogamic soil crust
    - Trampling disturbance and recovery 50:321-325
  - Lake Mead and Lake Mohave
    - Largemouth bass food habits 48:485-488
  - Lava Tube Caves
    - Invertebrates and zoogeographic significance 42:405-412
  - Mogollon Plateau
    - Biomass in montane forests 44:627-634
  - Montezuma Well, aquatic insects 49:85-88
  - Navajo National Monument
    - Bird community composition, Betatakin Canyon 41:298-309
    - Cryptogamic soil crusts 43:73-78
    - Plant communities 45:1-13

    - Subaerial algae 41:433-439
    - Vascular plants, checklist 38:19-30
  - Organ Pipe Cactus National Monument
    - Grass spider microhabitat 45:546-547
  - Pandora moth emergence 44:161-165
  - Rincon Mountains
    - Desert shrew habitat, distribution 49:140-141
  - Shivwits Plateau
    - Avifauna, Mt. Dellenbaugh Region 41:259-268
  - Walnut Canyon National Monument
    - Juniper mistletoe hosts 38:89
  - White fir dwarf mistletoe, distribution 36:461-462
  - White Mountains
    - Dwarf mistletoe, effects on spruce 46:685-689
    - Vegetation zones around a small pond 32:91-96
- Arizona, Central
  - Ponderosa pine, cone and conelet mortality 46:445-448
  - Ponderosa pine seeds, number and condition 46:449-451
  - Toad hybrid, Great Plains and red-spotted 50:371-372
  - Vegetation response to moisture gradient 39:161-176
- Arizona, Northern
  - Ant ecology 39:97-102
- Arizona-Sonoran Desert
  - Anuran sexual selection and mating 45:688-696
- *Artemia*, physical chemical parameters, five habitats 40:131-138
- *Artemisia*
  - *campestris* ***strutzae*** 28:147-156
  - *cana cana*
    - Sprouting and seedling establishment 50:201-207
  - *frigida* ***williamsae*** 28:147-156
  - Habitat types, Northern Nevada 33:225-242
  - Karyotypes 39:419-426
  - *nova*, nutritive content, winter 46:161-165
  - *tridentata*
    - Control attempts 40:157-164
    - Invasion by *Abies concolor*, California 35:319-324
    - Leaf morphology of subspecies 35:325-326
    - Rodent populations, Utah 35:191-202
  - *tridentata* ***pauciflora*** 45:99-104
  - *tridentata tridentata*
    - Selection by Sage Grouse 48:274-279
  - *tridentata vaseyana*
    - Seed planting depth 47:497-499
    - *Symphoricarpos oreophilus* associations, Northeastern Nevada 47:117-131
  - *tridentata wyomingensis*
    - Leaf development and longevity 47:227-230
    - Nitrogen availability, growth and photosynthesis 50:9-20
  - Wilt disease of unknown cause, Utah 41:184-191
- Arthropods
  - Arboreal
    - Coniferous forests, Western Oregon 48:327-333
  - Community dynamics
    - Mountain brush habitats 49:570-586
  - Desert, seasonal variation
    - Central Nevada 40:292-297
  - Effects on root:shoot ratio and biomass
    - Mountain shrub habitats, Wyoming 49:456-460
  - Litter decomposition
    - Mountain brush habitats 49:562-569
  - Nutrient cycling
    - Mountain brush habitats 49:134-139
  - Sampling problems after thermonuclear test 27:26-35
- Asclepiadaceae
  - *Asclepias*, systematics, New Mexico 49:100-103
- *Asclepias* ***sanjuanensis*** 49:100-103
- Aspens
  - Beaver foraging in, Central Utah 48:250-262
  - Trembling
    - Comparative successional roles, Southern Rocky Mountains 43:447-455
- Asteraceae
  - *Chrysothamnus*
    - Fossil, systematics, New Mexico 40:351-352
    - Systematics 44:416-420
    - Systematics, Utah 41:311-313
  - *Cirsium*, systematics 42:199-202
  - *Haplopappus*, systematics, Nevada 40:73-77
  - Systematics, keys, Utah 43:179-357
  - *Thelesperma*, systematics, Wyoming 43:749-750
  - *Vanclevea*, anatomy and systematics 34:151-160
- *Astragalus*
  - ***anserinus*** 44:263-264
  - ***atwoodii*** 37:103-104
  - ***debequaeus*** 45:31-33
  - *eremiticus* ***ampularioides*** 46:261-264
  - ***iselyi*** 34:305-310
  - *lentiginosus* ***wahweapensis*** 38:225-367
    - Population cycles, seed reserves, Henry Mountains, Utah 48:541-547
  - *limnocharis* ***tabulaeus*** 46:261-264
  - *monoensis*
    - Pollinators, impact of sheep grazing on 45:299-312
  - ***montii*** 38:1-18
  - ***piscator*** 45:551-552
  - *preussii* ***cutleri*** 46:254-260
  - ***stocksii*** 34:305-310
  - *subcinereus* ***basalticus*** 38:225-367
  - Systematics, Utah 34:180
- *Athene cunicularia*
  - Food habits
    - Southeastern Idaho 39:274-276
    - Southeastern Oregon 46:421-426
  - Foods, Conata Basin, South Dakota 45:287-290
  - Nesting success, Southeastern Idaho 45:81-84
- *Atriplex*
  - *canescens*
    - Inoculated with mycorrhizae 44:363-371
    - Isozymes 46:157-160
    - Winter crude protein 41:343-346
  - *canescens* ***gigantea*** 44:183-209
  - *confertifolia*

    Community ecology, Central Utah 46:348-357
    Elemental compartmentalization in seeds 47:91-95
  suckleyi
    Forage quality on bentonite mine spoil 50:57-62
  triangularis, compartmentalization in seeds 47:91-95
Auriparus flaviceps
  Body composition, Clark County, Nevada 31:66-68
Author index, Utah plant names 42:385-394
Auturus ***becki*** 11:27-35
Avalanche paths, vegetation patterns
  Northern Rockies, Montana 44:453-458

B

Badgers
  Associations with coyotes 41:347-348
  Holocene predation of Uinta ground squirrel 50:385
  Intercanine crown distances
    South Dakota 42:601-602
  Winter stomach contents, South Dakota 43:492-493
Bagous
  angustus 14:73-78
  blatchleyi 4:1-38
  chandleri 4:1-38
  dietzi 14:73-78
  floridanus 4:1-38
  lengi 4:1-38
  longirostrus 4:1-38
  texanus 4:1-38
  tingi 4:1-38
Baker County, Oregon, herpetology 18:63-65
Balaena mysticetus, parasites 47:355-372
Ball Mountain, California
  Butterflies, biogeography 46:336-347
Ballophilus ***liber*** 13:75-85
Barisia, significance of scale characters 34:257-266
Basidiomycetes
  Juniper decaying, systematics
    Arizona 38:42-48
    Arizona, keys 35:288-304
Basilia
  jellisoni 24:107-115
  mimoni 24:107-115
  Systematics, Venezuela 37:221-224
Bass
  Largemouth
    Food habits in Lake Mead and Lake Mohave, Arizona-Nevada 48:485-488
  White, spawning ecology in Utah Lake 28:63-69
Bat boxes, House Wren use 43:456
Bathyodontus cylindricus 10:45-50
Bats
  Colorado oil shale region, distribution 43:554-560
  In Spotted Owl pellets, Southern Arizona 50:197-200
  Spotted
    Notes from Southwest Utah 34:254-256
    Roosting behavior, Washington County, Utah 35:121-122
Bear Lake Basin, Utah-Idaho, hydrology 46:690-705
Bear River marshes, Utah
  Unusual winter bird visitors or late migrants 3:51-53
Bears, Great Basin black, Carson Range, Nevada
  Co-occupancy of a den 49:390-391
Beavers
  Dam site selection, Eastern Oregon 50:273-281
  Foraging patterns in aspens 48:250-262
Beck, D Elden 27:230-239
Bee, Robert G. 3:86-90
Beeflies, Nevada Test Site 25:5-11
Bees
  Nevada Test Site 29:20-24
  Pollen-collecting, sweetvetch
    Grand Teton National Park 47:314-318
  Pollinators of *Astragalus monoensis* 45:299-312
Beetles
  Aspen bark
    Bionomics 37:105-127
    Emergence data, artificial rearing media 39:129-132
  Colorado ground
    Rotger collection, University of Colorado 47:631-637
  Douglas-fir
    Broods on spruce budworm defoliated trees 48:348-351
    Emergence, attack densities, hosts, Northern Colorado 50:333-338
  Ecology of populations near Lake Powell 39:89-96
  Mexican bean, damage in Utah, 1943 4:61
  Mountain pine cone
    Cone production and population levels 44:310-312
Benton Hot Springs, California
  Vascular plant communities 47:583-591
Bentonite mine spoil, amended
  Forage quality of *Atriplex suckleyi* 50:57-62
Betatakin Canyon, Arizona
  Bird community composition 41:298-309
Bibiocephala nigripes 25:1-3
Bibliography
  Colorado, vegetation 43:45-64; 44:677-680
  Eumeces septentrionalis 49:525-534
  Montana, vegetation description 48:301-323
  Nevada, ornithology 28:49-60
  Nevada and Utah, vegetation description 50:209-242
  Nevada Test Site, ecological research 26:79-86
  New Mexico, grass taxonomy and types 50:73-82
  Plecoptera, North America 46:383-397
  Southwest local floras, 1920-1989 42:105-112
  Utah, aquatic biology 22:32-53
Big Soda Lake, Nevada
  Primary productivity 38:187-192
  Zooplankton orientation to the oxycline 49:535-539
Bighorn Canyon National Recreation Area
  Vascular plants, checklist 45:734-746
  Vertebrates
    Checklist, distribution 47:512-521
Biological investigations
  Great Salt Lake, Utah, summary 34:221-229

- Biomass
  - Predicted by regression 45:94-98
  - Predictions, conifer forests 37:395-401
- Biotic communities
  - Southern Wasatch and Uinta mountains, Utah 6:1-124
- Birds
  - Antarctic 2:122-124
  - Aquatic, White River, Utah 45:113-116
  - Bear River marshes, Utah
    - Unusual winter visitors or late migrants 3:51-53
  - Breeding records, Utah 3:61-85
  - Cavity-nesting, tree use, Wyoming 46:358-360
  - Cold Spring Mountain
    - Northwestern Colorado 46:651-655
  - Community composition, Betatakin Canyon
    - Navajo National Monument, Arizona 41:298-309
  - Distribution and breeding, Utah and Idaho 43:717-727
  - East Central Nevada
    - Bristlecone pine stand 44:272-276
  - Fossil, Oreana local fauna
    - Owyhee County, Idaho 46:763-768
  - Grazing and passerine breeding
    - Great Basin 46:567-572
  - Great Salt Lake islands, checklist 37:247-251
  - Hells Canyon, checklist 49:279-287
  - Kawich Mountains, Nevada 16:32-33
  - Mortality and high insect populations 28:200
  - Mountain dwelling, nesting habits, Utah 2:1-8
  - Mt. Dellenbaugh
    - Shivwits Plateau, Arizona 41:259-268
  - Nevada, distribution 14:15-18
  - San Juan County, New Mexico 37:489-500
  - Scoria rock outcrop use 47:625-630
  - Shadscale habitat, Central Nevada 50:295-298
  - Southern Nevada, uncommon records 26:41-42
  - Southwestern Idaho, checklist 43:728-738
  - Temperature-related behavior
    - Mojave Desert 42:232-240
  - Uinta Basin, Utah 18:23-25
  - Uinta Mountains and Basin, Utah 18:1-22
  - Uintah County, Utah
    - Checklist, distribution 44:584-620
  - Utah 33:243-245
  - Water, Rock Island, Utah Lake 6:127-128
  - Water impoundment use
    - Northern Great Plains 48:353-357
  - Wintering habits, Nevada Atomic Test Site 22:30-31
- ***Bisancora rutriformis*** 41:349-359
- Bitterbrush
  - Antelope
    - Impact of the 1975 Wallsburg, Utah fire 40:299-302
    - Increased summer consumption by mule deer 44:572-574
  - *Phigalia plumogeraria* control on, Utah 41:290-297
- Blackbirds, Yellow-headed
  - Habitat and reproductive strategy 38:85-88
  - Territory establishment, maintenance, Utah 1:75-91
- Blackbrush community
  - Habitat relationships, Southwestern Utah 45:321-326
- Blaisdell, Frank Ellsworth, Sr. 7:17-20
- Blatchley, Willis Stanley 2:33-35
- Blazzard, John E., mammal collection 1:146
- Bluebird, Western, leucism 48:75-77
- Bobcats, Washington
  - Autumn and winter food habits 44:70-74
- ***Boleodorus*** (Nematoda) 2:37-85
  - ***clavicaudatus*** 2:37-85
  - ***thylactus*** 2:37-85
- *Bolitoglossa*, osteology 18:85-100
- *Boliviela*
  - ***bispinosa*** 48:232-249
  - ***paraortha*** 48:232-249
- *Bombylius*
  - ***abdominalis*** 35:407-418
  - ***aestivus*** 35:407-418
  - ***auriferoides*** 35:407-418
  - ***heximaculatus*** 35:407-418
  - *lancifer* ***kanabensis*** 35:407-418
  - ***montanus*** 35:407-418
  - ***nigriventris*** 35:407-418
  - ***pallescens*** 13:17-27
- Bonneville Basin, Utah
  - Pocket mice reproduction 50:361-365
- Bonneville Basin, Western
  - Status of *Salmo clarki* subspecies 38:193-202
- *Bootherium*, Pleistocene, systematics 47:239-251
- Boraginaceae
  - *Cryptantha*
    - Systematics 29:28-30
    - Systematics, Nevada 42:196-198
    - Systematics, Utah 28:195-198; 42:203-204
  - *Plagiobothrys*, systematics, keys 34:161-166
  - Systematics, keys, Southwest 39:293-350
- *Boraria* ***monticolens*** 11:19-26
- Botflies
  - Larvae, parasitizing *Peromyscus*
    - Northern Colorado 36:481-482
  - Rodent, field behavior and seasonal activity
    - Central Washington 34:247-253
- *Bothinodroctonus*
  - ***indicus*** 48:188-195
  - ***setosus*** 48:188-195
- *Bothrosternus*
  - ***definitus*** 28:88-110
  - ***hirsutus*** 45:266-275
- Bottle feeding, mule deer fawns 46:217-219
- Bottle Hollow Reservoir, Utah
  - Algal populations, checklist, distribution 42:205-218
- Brachiosauridae
  - Late Jurassic, Utah and Colorado 47:592-608
- *Brachylagus idahoensis*
  - Alarm call 41:158-160
  - Colorado River drainage 47:231-233
- *Brachylophus* ***brevicephalus*** 30:166-172
- *Brachyprotoma* ***brevimala*** 45:337-390
- Brassicaceae, *Lepidium*, systematics, Utah 27:177-181
- *Braya humilis humilis*, ecology, Colorado 46:728-735

Bredin-Archbold-Smithsonian Biological Survey
  Lace bug collections 28:161-171
Brevicapitorus elongatus 49:96-99
Brigham Young University Entomological Collection
  List of insect type specimens 29:150-164; 29:183-205; 34:317-322
Brigham Young University Museum of Natural History
  Catalogue of fish, amphibian, and reptile types 30:219-226
Bryant, Owen, vertebrate collections 9:47-49
Bryce Canyon Breaks, Utah, vegetation 43:701-712
Bryce Canyon National Park, Utah
  Drosophila pseudoobscura, release 47:32-37
  Vascular flora, checklist 48:352
Bryobia ***neoribis*** 36:57-64
Buccal floor, reptiles, summary 42:273-349
Budworms, western spruce
  Foliage age and food utilization 46:169-172
  Natural enemies, Rocky Mountains 47:319-321
Bufo
  alvarius, type specimen 28:70-72
  boreas boreas, breeding behavior
    Western Montana 31:109-113
  cognatus X punctatus, Central Arizona 50:371-372
Bulldozing, Utah pinyon-juniper
  Effect on browse species 46:508-512
Bunchgrass
  Effects of burning and clipping
    Eastern Oregon 50:115-120
  Regression methods
    Biomass estimation 49:373-380
Burning, prescribed
  Soil water and temperature response 44:558-562
Burrow plugging
  Prairie dog response to Siberian polecats 44:447-449
Buteo
  regalis, population dynamics
    West Central Utah 37:411-425
  swainsoni
    Ground nesting, aggressive behavior 39:253-254
Butterflies
  Ball Mountain, California, biogeography 46:336-347
  Castle Peak, California 37:443-452
  Mourning cloak, phenology, California 46:112-116
  Painted lady
    Rare aberrant forms, Utah 31:256-260
    Migration 2:104
  Pierid, aberrant populations
    Photoperiodic responses 35:310-316
  Tortoise-shell, migration, Utah 13:8
  Zoogeography, Great Basin 47:186-201
Bylas Springs, Arizona
  Sonoran topminnows, management 50:265-273

C

C3, C4 plant species, ecology, Central Utah 46:140-147
Cache County, Utah
  Spiders, size and seasonal activity 44:104-110
Cactaceae
  Opuntia, systematics, Utah 43:700
  Sclerocactus
    Systematics, Nevada 45:553-555; 46:677-678
  Systematics, keys, Utah 44:52-69
Cactopinus
  atkinsoni 43:647-659
  burjosi 43:647-659
  cactophthorus 17:105-110
  granulatus 43:647-659
  mexicanus 27:36-57
  setosus 43:647-659
  spinatus 17:105-110
Cactus, barrel
  Slope preference in Southwestern Utah 44:133-139
Caeculus ***mariae*** 17:27-29
California
  Benton Hot Springs, Mono County
    Vascular plant communities 47:583-591
  Castle Peak, butterflies 37:443-452
  Colorado Desert, *Spaniacris*, bioecology 35:113-120
  Costal fen hydrology 37:57-66
  Cowboy Hot Spring, Mono County
    Diatom flora 46:612-624
  Death Valley
    Pacific tree frog, albino 29:111
    Herpetofauna 23:119-128
  Grass Lake
    Ambystoma, relictual population 38:429-437
  Mason Fen, peat depth 36:101-107
  Mohave Desert, coniferous woodlands
    Pleistocene-Holocene 36:227-238
  Mono Lake, salt grass invasion 45:542-545
  Northern Sierra Nevada
    Prehistoric bighorn sheep 33:221-224
  Nymphalis antiopa, phenology 46:112-116
  Panamint Valley
    Dipodomys merriami, burrowing habits 31:190-192
  Pinyon-juniper woodland densities 46:178-184
  Ruth Reservoir
    Fish distribution and abundance 42:529-540
  Sagehen Creek
    Coexistence of two *Catostomus* species 49:540-551
  Sagehen Creek Basin
    Trichoptera species, emergence, habitat 49:186-197
  San Mateo County
    Tick host-parasite relationships 24:1-6
  Saratoga Springs
    Lizards, environmental response 30:146-165
  Sequoia National Park
    Carex exserta, soil nutrients 45:61-66
  Siskiyou County
    Butterflies, biogeography 46:336-347
  Upper Walker River
    Vascular flora, checklist 43:93-130
  Warner Mountains
    White fir invasion of big sagebrush 35:319-324

  White Mountains
    Bristlecone pine and Clark's Nutcracker 44:357-360
California, Northeastern
  Genetics of hybridized pocket gophers 44:431-440
  Soil compaction following logging 48:117-120
California, Northern
  Douglas-fir dwarf mistletoe on Pacific silver fir 47:161-162
California, Southern
  Echinocereus engelmannii
    Ecomorphology 42:353-359
  Echinocereus triglochidiatus
    Ecomorphology 42:353-359
Callibaetis, food 41:431-432
Calligrapha multipunctata multipunctata
  Life history 18:101-103
Callisaurus draconoides, ecology 47:175-185
Callistopsyllus, systematics 39:351-418
Calodicia ***circulata*** 48:232-249
Camissonia ***atwoodii*** 46:254-260
Camp Floyd State Park, Utah
  Cryptogamic soil crusts 46:632-640
Canada
  Alberta
    Riverbottom forest community 36:243-271
    Lee Creek Valley, vascular plants, checklist 39:277-283
    Lethbridge, rattlesnakes, cannibalism 31:49-50
Canids, wild, radio transmitter implants 45:567-570
Canis latrans
  Food habits on Utah deer herds 43:432-437
  Prey, energy and protein content, Idaho 46:274-276
  Seasonal foods, Southeastern Idaho 42:45-49
  Summer food habits
    Central Wyoming 41:449-456
    River of No Return Wilderness Area, Idaho 50:63-65
Canopy cover, estimating
  Spherical densiometer and ocular methods 48:224-227
Canyon Mountains, Utah
  Vascular plant checklist 44:277-295
Canyonlands National Park, Utah
  Ecological distribution of rodents 39:199-205
Capitol Reef National Park, Utah
  Utah prairie dog reestablishment 42:517-523
Capnia, systematics, distribution, keys
  North America 49:289-363
Carebareia johnstoni 37:501-509
Carex
  exserta, soil nutrients
    Sequoia National Park, California 45:61-66
  nebraskensis, dry-year grazing 47:422-426
Carnivores, small, survey techniques 43:438-440
Carphobius ***pilifer*** 43:647-659
Carphoborus
  bicornis 46:265-273
  lautus 48:188-195
  perplexus 20:59-69
Carphotoreus alni 33:169-188
Carson Range, Nevada
  Great Basin black bear den co-occupancy 49:390-391
Casa Grande National Monument, Arizona
  Mesquite 31:153-159
Cascade Range, Oregon, *Felis concolor*, food 45:77-80
Castle Cliffs, Utah, vegetation patterns 45:535-541
Castle Peak, California, butterflies 37:443-452
Castor canadensis
  Dam site selection, Eastern Oregon 50:273-281
Catalogue, fish, amphibian, and reptile types
  Brigham Young University 30:219-226
Caterpillars, western tent
  Length of egg masses 41:465-466
Cathartes aura, roosting site decline
  Oregon 46:305-306
Cathetosaurus lewisi 48:121-145
Catostomus
  catostomus
    Parasites, Yellowstone Lake, Wyoming 47:259-275
    Parasitized by *Trichophrya*, Yellowstone Lake 45:255-265
  Coexistence of two species
    Sagehen Creek, California 49:540-551
  discobolis, parasites, Southern Utah 40:149-156
  latipinnis
    Growth and reproduction, Colorado River 45:281-286
    Parasites, Southern Utah 40:149-156
  tahoensis, reproductive ecology
    Pyramid Lake, Nevada 38:181-186
Cattails, decline, Farmington Bay, Utah 37:24-34
Caudata, Oklahoma, distribution 11:87-90
Cedar Mountain Formation, Utah-Colorado
  Lower Cretaceous flora 44:231-256
Cenocephalus ***epistomalis*** 26:45-70
Centaurium namophilum ***nevadense*** 41:192-197
Centipeds
  Lithobiid, systematics, North America 11:115-118
  Systematics, United States 11:27-35
Centrocercus urophasianus
  Big sagebrush, selection 48:274-279
  Habitat use by breeding males 49:404-407
Ceratium hirundinella
  Competitive displacement, distribution 39:245-252
Ceratoides
  lanata
    Grazing pressure, Kane County, Utah 46:148-156
  lanata ***ruinina*** 44:183-209
Cerceris, prey and nests of seven species 38:59-63
Cercocarpus montanus, Chadron, Nebraska 37:97-99
Cestoda, *Ophiotaenia*, systematics 41:445-448
Cestodes
  Infections, Central Utah 46:208-216
  Prevalence in Central Utah sheep dogs 42:65-66
Chaco Canyon, New Mexico
  Spatial and temporal variability of vegetation 49:113-122

- Chadron, Nebraska, *Cercocarpus montanus* 37:97-99
- *Chaetophloeus*
  - ***confinis*** 43:647-659
  - ***minimus*** 27:79-97
  - ***pouteriae*** 46:265-273
  - ***struthanthi*** 27:79-97
- Chaining, Utah pinyon-juniper
  - Effect on browse species 46:508-512
- Chandler, Harry Phylander 15:50-54
- *Chandlerella* ***robinsoni*** 36:445-457
- *Charina bottae*, reproduction, Utah 1:27-30
- *Chasmistes cujus*
  - Life history, Pyramid Lake, Nevada 45:571-603
- *Cheilotrichia*
  - ***aklavikensis*** 26:1-8
  - ***tanneri*** 30:232-241
- Chelonians, fossil, Idaho, Upper Pliocene 29:82-87
- Chenopodiaceae, systematics, keys, Utah 44:183-209
- *Chenopodium capitatum* ***parvicapitatum*** 44:183-209
- *Chernokrilus misnomus*, nymph 44:373-415
- Chihuahuan Desert, New Mexico
  - Tiger salamander, life history 31:193-212
- Chilopods
  - Geophiloid, systematics
    - Hawaii and Pacific Islands 13:75-85
  - Scolopendrid, systematics
    - Northern Andes, South America 17:30-41
  - Tampiyidae, systematics, keys 25:39-42
- Chimney Creek, Nevada
  - Lahontan cutthroat trout, spawning behavior 47:480-487
- Chipmunks, cliff
  - Food preferences, Logan Canyon, Utah 31:182-188
  - Genetic variation, Western Utah 47:551-561
- *Chiracanthium mildei*, bite of human described 40:116
- Chokecherry, black knot disease, Utah 44:579-583
- *Chordeiles*, distribution, Utah 1:93-96
- *Choristoneura occidentalis*
  - Douglas-fir defoliated by, and *Dendroctonus pseudotsugae* broods 48:348-351
  - Foliage age and food utilization 46:169-172
  - Natural enemies, Rocky Mountains 47:319-321
- *Chramesus*
  - ***atkinsoni*** 41:121-128
  - ***bicolor*** 27:79-97
  - ***bispinus*** 42:223-231
  - ***demissus*** 27:79-97
  - ***exilis*** 43:647-659
  - ***exul*** 43:647-659
  - ***incomptus*** 27:79-97
  - ***minulus*** 29:113-128
  - ***punctatus*** 27:79-97
  - ***securus*** 43:647-659
  - ***setosus*** 20:59-69
  - ***tibialis*** 43:647-659
  - ***vastus*** 27:79-97
  - ***vitiosus*** 29:113-128
- Chromosome counts, plants, Western America 33:19-25
- *Chrysemys idahoensis* 29:82-87
- *Chrysomyxa pirolata* on *Picea pungens*
  - Utah 42:262-272
- *Chrysothamnus*
  - Computer analysis of leaf cross sections 48:334-347
  - *nauseosus*
    - Specificity of tephritid gall forms 39:81-87
  - *nauseosus albicaulis*
    - Chloroplast ultrastructure 46:573-576
    - Photosynthesis, high rates 45:520-526
  - *nauseosus* ***iridis*** 41:311-313
  - *nauseosus turbinatus*
    - Seasonal changes 48:1-8
  - *nauseosus* ***uintahensis*** 44:416-420
  - *nauseosus viridulus*
    - Seed germination 47-220-226
  - ***pulchelloides*** 40:351-352
  - *viscidiflorus*
    - Systematics, keys 40:117-120
- *Chrysotus* ***silvicolus*** 11:11-17
- Chubs
  - Borax Lake
    - Feeding ecology, Southeastern Oregon 40:101-114
  - Fish Creek Springs tui
    - Status and distribution 46:441-444
  - Flathead, biology, Montana 45:332-336
  - Humpback
    - Yampa and Green Rivers, Utah 50:257-264
  - Lahontan tui
    - Biology, Walker Lake, Nevada 42:60-64
  - Least, spawning 40:139-140
  - Roundtail, Yampa and Green Rivers, Utah 50:257-264
  - Tui
    - Biology in Walker Lake, Nevada 45:784-788
    - Food of larvae, Pyramid Lake, Nevada 43:175-178
    - Reproductive biology, Pyramid Lake, Nevada 38:203-207
    - Seasonal growth, Pyramid Lake, Nevada 43:713-716
  - Utah, Pleistocene, Corrine, Utah 49:131-133
- Chukars, radio transmitter attachment 49:632-636
  - Effect on mating 50:379-380
- Church Mountains, Utah
  - Vascular plant checklist 44:277-295
- *Cibolacris* ***samalayucae*** 21:29-33
- Cicindelidae
  - Systematics
    - South Pacific Islands 11:47-51
    - Western United States 11:47-51
- *Cicindella*, Idaho, checklist 44:159-160
- Ciconiiforms
  - Nesting, status and distribution, Wyoming 48:290-297
- *Cimbocera* ***petersoni*** 2:29-32
- *Cinara*
  - ***caliginosa*** 21:17-19
  - ***enigma*** 14:11-13
  - ***lunata*** 21:20-22
  - ***minuta*** 14:11-13
  - ***osborni*** 3:5-8

Systematics, keys, North America 21:35-50
  wahluca 12:57-61
Cinara puerca, morphology 14:83-86
Circotettix rabula, substrate color matching 34:60-70
Cirsium
  eatonii ***harrisonii*** 42:199-202
  eatonii ***murdockii*** 42:199-202
  ownbeyi 42:199-202
  scariosum ***thorneae*** 42:199-202
  virginensis 42:199-202
Clark County, Nevada
  Verdin, body composition 31:66-68
Clark's Nutcracker
  Bristlecone pine relationship, White Mountains, California 44:357-360
Clearwater drainage, Idaho
  Sculpins, morphometry, keys 38:115-122
Clearwater River Basin, Idaho
  Sculpin distribution 39:59-62
Cleidogona
  mandeli 12:13-34
  punctifer 12:13-34
  tajumulco 12:13-34
Clemmys owyheensis 29:82-87
Cleomella palmerana ***goodrichii*** 46:261-264
Clethrionomys
  californicus, mycophagy 48:269-273
  gapperi
    Microhabitat selection 48:216-223
    Mycophagy 48:269-273
    Short-term effects of logging on 40:183-189
Cliffrose
  Habitat, community ecology, Central Utah 47:132-151
  Stem circumference, diameter and age
    Utah 47:334-338
Climacia californica
  Water quality relationships, Idaho 45:391-394
Clinohelea
  longitheca 35:275-287
  pseudonubifera 35:275-287
Clusiaceae, *Sahniocarpon*, systematics, India 47:527-535
Cnemidophorus tigris
  Food habits, Southeastern New Mexico 45:527-534
Cnemonyx
  cornutus 43:647-659
  equihuai 43:647-659
  euphorbiae 46:265-273
  evidens 43:647-659
  furvescens 39:133-142
  nebulosus 43:647-659
  parvicornis 43:647-659
  protivorus 39:133-142
  squamifer 39:133-142
  visimiacolens 39:133-142
Cnesinus
  adusticus 27:79-97
  annectens 27:79-97
  aquihuai 42:223-231
  atavus 28:88-110
  atrocis 42:223-231
  atrodeclivis 28:88-110
  bicornus 27:79-97
  carinatus 27:79-97
  colombianus 27:79-97
  degener 28:88-110
  denotatus 28:88-110
  discretus 45:266-275
  electinus 27:79-97
  elegantis 27:79-97
  foratus 27:79-97
  frontalis 28:88-110
  gibbosus 28:88-110
  gibbulus 28:88-110
  meris 42:223-231
  minitropis 28:88-110
  minor 45:266-275
  myelitis 27:79-97
  niger 27:79-97
  perplexus 28:88-110
  pilatus 35:21-32
  prominulus 37:207-220
  retifer 27:79-97
  squamosus 28:88-110
Coal mine spoils
  Long-term plant survival 41:271-273
  Southwest, reclamation 44:441-446
Coelidia
  cochloea 43:669-674
  panamensis 43:669-674
  retrorsa 43:669-674
  simplex 43:669-674
  tortula 43:669-674
Coenia ***alpina*** 35:65-85
Coleogyne ramosissima
  Community habitat relationships 45:321-326
Coleoptera
  Aquatic, systematics, Nevada 10:66-70,11:52
  Araeoschizus, systematics 6:125-126
  Buprestidae, systematics, Nevada Test Site 29:11-19
  Carabidae
    Rotger collection, University of Colorado 47:631-637
  Cerambycidae, systematics, Idaho 29:88-95
  Cerambycoidea, systematics, keys, Nevada 11:97-104
  Cicindella, Idaho, checklist 44:159-160
  Cleridae, systematics, Nevada Test Site 29:11-19
  Cnesinus, systematics, keys
    North and Central America 28:88-110
  Corthylus, systematics, Americas 34:181-202
  Craniotus, systematics 23:167-170
  Curculionidae
    Systematics 1:31-32; 20:23-28
    Systematics, Western United States 2:29-32
  Dactylipalpus, systematics, Philippine Islands 21:8-9
  Dendroctonus, systematics, keys 23:1-117
  Diplotaxis, systematics 1:127-137

Dytiscidae, systematics, keys, Utah 22:54-75
Elaphrus, systematics 2:137-138
Eleodes, systematics, checklist 21:55-78
Enoclerus, systematics, Great Basin 7:21-22
Eschatomoxys
  Systematics, Glen Canyon, Utah 19:63-66
Eucyllus, systematics 19:53-55
Eupagiocerus, systematics, keys 25:31-35
Haliplus, systematics, Nevada 49:89-91
Histeridae, systematics, checklist, Nevada 7:7-10
Hydronomi, systematics, keys 4:1-38
Idaho National Engineering Laboratory
  Checklist 46:287-293
Microcorthylus, systematics, Americas 33:265-275
Microrhopala
  Systematics, keys, North America 43:597-618
Miloderes, systematics 34:291-296
Miloderoides
  Systematics, Western United States 3:23-26
Nevada Test Site, checklist 34:218-220
Pelecyphorus, systematics 22:110-113
Phyllotrox, systematics 36:463-466
Pityoborus, systematics, keys 18:46-56
Pityophthorus
  Systematics, North America 24:59-70; 38:71-84
  Systematics, North America, keys 45:467-475; 45:476-482; 46:641-645; 46:679-684
Platypodidae
  Systematics 29:113-128; 33:77-90; 41:121-128
  Systematics, Neotropical Region 26:45-70
  Systematics, synonymy 26:17-33
Platypus
  Systematics, Americas 31:243-253
  Systematics, North America 18:37-40
Pseudoxylechinus
  Systematics, Asia 46:465-467
  Systematics, India 46:468
Rhynchophora, male genitalia, systematics 8:1-35
Scarabaeidae, Nevada Test Site 25:77-79
Schedlarius, systematics, Central America 17:103-104
Scolytidae
  American, introduced and exported 37:67-74
  Checklist, Idaho 47:375-382
  Checklist, Montana 49:381-386
  Systematics 22:76-82; 29:113-128; 32:40-54; 33:77-90; 36:425-444; 40:89-97; 41:121-128; 44:223-230; 45:266-275; 46:461-464; 48:188-195; 48:196-201; 48:31-38; 49:167-185
  Systematics, Americas 34:277-290; 35:21-32; 31:140-152; 32:190-201; 33:169-188; 34:135-150; 35:391-401; 36:347-365; 37:207-220; 37:383-394; 37:511-522; 38:397-405; 39:133-142; 40:353-358; 42:223-231; 43:647-659; 44:113-119; 46:265-273
  Systematics, Colombia 21:1-7
  Systematics, Mexico 27:36-57; 47:547-550
  Systematics, Mexico and Florida 17:105-110
  Systematics, Mexico and Texas 19:1-7
  Systematics, Neotropical Region 21:87-107; 27:119-141; 27:79-97; 28:1-15
  Systematics, synonymy 26:17-33
  Systematics, Western North America 20:59-69; 31:69-76
Sitona, systematics, Americas 47:168-174
Systematics, Utah 2:99-104
Collembola
  Checklist
    Idaho 16:1-6
    Utah 16:7-8
  Systematics, keys 4:39-48
  Utah 13:43-46
Colorado
  Braya humilis humilis, ecology 46:728-735
  Bristlecone pine germination 32:235-237
  Clark's Grebe, breeding records 46:581-582
  Colorado River, *Helobdella stagnalis* 44:361-362
  Delta County, *Symbos cavifrons* 45:455-461
  Dryosaurus altus, Upper Jurassic 33:129-132
  Invertebrates, alpine lake and stream chain 47:500-511
  Laramie Basin, vegetation, postglacial 43:377-384
  Martes americana, winter feeding habits 46:166-168
  Mesa Verde National Park, fleas 26:76-78
  Moffat County, presettlement vegetation 45:747-777
  Mosquito records, annotated list 9:65-75
  Northern San Juan Mountains
    Tundra vegetation 45:87-93
  Odonata, checklist 48:96-101
  Piceance Basin
    Presettlement vegetation 43:687-699
    Small mammal food habits 44:145-150
  Pine marten, winter feeding habits 46:166-168
  Preliminary vegetation classification 44:647-676
  Rare flora 48:434-484
  Rocky Mountain National Park
    Peromyscus maniculatus fleas 43:168-174
  San Luis Valley
    Background radiation and endemic fauna 19:37-42
  Thomomys talpoides, albinism 31:181
  Upper Jurassic, mammalian humerus 43:551-553
  Vascular plant distributional records 38:208-210
  Vegetation, bibliography 43:45-64; 44:677-680
  West Elk Mountains
    Alpine vascular flora, checklist 47:152-160
  Zapus princeps, home range 37:87-90
Colorado Desert, California
  Spaniacris, bioecology 35:113-120
Colorado River, Colorado
  Helobdella stagnalis 44:361-362
Colorado River, lower
  Xyrauchen texanus, ecology and recruitment 49:71-78
Colorado River drainage, pygmy rabbits 47:231-233
Colorado, Northern
  Botfly larvae parasitizing *Peromyscus* 36:481-482
  Douglas-fir beetles
    Emergence, densities, hosts 50:333-338
Colorado, Northwestern
  Bats of the oil shale region 43:554-560

  Cold Spring Mountain, birds 46:651-655
  Pinyon-juniper woodlands
    Spatial pattern and interference 50:313-320
Colorado, West Central
  American swallow bugs, Barn and Cliff Swallow nest occupants 47:345-346
Colorado, Western
  Dinosaurs, Uncompahgre fauna 45:710-720
  Riparian vegetation classification 49:214-228
  Sauropod dinosaurs, Upper Jurassic 45:697-709
Coluber constrictor mormon, reproduction, Utah 33:202
Comandra umbellata
  Ecology, Western Wyoming 49:650-655
Community dynamics
  Arthropod, mountain brush habitats 49:570-586
Competition
  Rodents and harvester ants, cold desert 39:267-273
Compositae
  Artemisia, systematics, keys 45:99-104
  Erigeron, systematics, Nevada 48:495-498
  Haplopappus, systematics, Utah 43:371-372
  Hymenoxys, systematics, Utah 43:373-374
  Perityle, systematics, Utah 43:373-374
  Stephanomeria, systematics, Utah 43:375
  Systematics, keys, Utah 43:179-357
  Thelesperma, systematics, Utah 43:369-370
  Townsendia
    Systematics, keys, Utah 30:23-52
    Systematics, Utah 43:369-370
Conifer forests
  Biomass and nutrient exports 37:395-401
Coniferales, *Agathoxylon*, systematics 46:559-566
Coniferous forests
  Arboreal arthropods, Western Oregon 48:327-333
Conifers
  Distribution, Utah 31:177-180
  Great Basin 31:85-89
Conophorus ***sackenii*** 13:17-27
Conophthorus
  cembroides 31:69-76
  conicolens 37:207-220
  echinatae 38:397-405
  mexicanus 22:76-82
  michoacanae 40:353-358
  teocotum 40:353-358
Conorhinopsylla, systematics 39:351-418
Contopus
  sordidulus
    Geographic variation, north of Mexico 37:453-456
  virens
    Geographic variation, north of Mexico 37:453-456
Cophosaurus texanus, ecology 47:175-185
Copper toxicity, *Synechococcus lividus* 41:255-258
Cormocephalus
  anechinus 17:30-41
  tingonus 17:30-41
Cormorant, Double-crested, breeding, Utah 37:1-23
Corthycyclon
  caliginis 34:135-150
  furvus 34:135-150
  morulus 34:135-150
  tardus 34:135-150
Corthylocurus (Coleoptera) 26:17-33
  debilis 34:135-150
Corthylus
  additus 34:181-202
  brunneus 34:181-202
  calamarius 34:181-202
  calmicolens 34:181-202
  cannularius 34:181-202
  cecropii 35:21-32
  cirritus 34:181-202
  comosus 34:181-202
  concisus 34:181-202
  consimilis 34:181-202
  convexifrons 46:265-273
  diligens 34:181-202
  donaticus 34:181-202
  exiguus 44:113-119
  granulifer 34:181-202
  insignis 34:181-202
  lustratus 44:113-119
  micacirrus 44:113-119
  minimus 34:181-202
  nanus 39:133-142
  nolenae 34:181-202
  oculatus 34:181-202
  petilus 27:36-57
  pumilus 34:181-202
  pygamaeus 34:181-202
  retusifer 34:181-202
  retusus 34:181-202
  senticosus 46:265-273
  sentosus 46:265-273
  sentus 34:181-202
  serratus 34:181-202
  simplex 34:181-202
  sobrinus 34:181-202
  spinosus 34:181-202
  splendens 27:119-141
  strigilis 34:181-202
  subserratus 34:181-202
  trucis 34:181-202
  truncatus 45:266-275
  trunculus 34:181-202
  villifer 34:181-202
  zelus 34:181-202
Corvus corax
  Nesting on interstate highway overpasses 48:64-67
  Unusual social feeding and soaring 45:150-151
Cottam, Clarence 35:231-239
Cottus
  bairdi, parasites, Utah 47:13-21
  Distribution, Clearwater River Basin, Idaho 39:59-62
  greenei, distribution
    Hagerman Valley, Idaho 44:324-326

  Morphometry, Clearwater drainage, Idaho 38:115-122
Cougars, winter food habits, Oregon 43:425-428
Cowania
  Intergeneric hybrids, Arizona 44:484-486
  mexicana stansburiana
    Habitat and community relationships, Central Utah 47:132-151
    Stem circumference, diameter and age, Central Utah 47:334-338
Cowboy Hot Spring, California
  Diatom flora 46:612-624
Coyotes
  Associations with badgers 41:347-348
  Diets when sympatric with red foxes 41:251-254
  Food habits on Utah deer herds 43:432-437
  Prey, energy and protein content, Idaho 46:274-276
  Pronghorn antipredatory behavior 43:88-92
  Seasonal foods, Southeastern Idaho 42:45-49
  Summer food habits
    Central Wyoming 41:449-456
    River of No Return Wilderness Area, Idaho 50:63-65
Craniotus ***blaisdelli*** 23:167-170
Crataegus douglasii ***duchesnensis*** 42:1-44
Craters of the Moon, Idaho
  Kipukas and species numbers 42:113-119
Crayfish
  Utah, distribution 46:625-631
  Wyoming, checklist, management 48:370-372
Crenichthys
  baileyi
    Foods and feeding periodicity 49:249-251
  nevadae
    Response to temperature 40:359-360
Cretaceous, Lower
  Cedar Mountain Formation flora 43:394-402
Cromerus ***excelans*** 13:91-99
Crotalus lepidus ***maculosus*** 32:16-24
Crotaphytus
  collaris ***bicinctores*** 32:25-34
    Observation of voice 34:276
  insularis ***vestigium*** 32:25-34
  wislizeni
    Systematics, Great Basin 37:225-240
  wislizeni ***maculosus*** 37:225-240
  wislizeni ***neseotes*** 28:183-194
  wislizeni ***punctatus*** 23:129-148
Cruciferae
  Draba, systematics 43:441-444
  Physaria, systematics, keys, Utah 33:31-36
  Systematics, keys, Utah 37:279-365
Cryphalogenes (Scolytidae) 40:89-97
  euphorbiae 40:89-97
  exiguus 40:89-97
Cryphalus
  dipterocarpi 49:167-185
  felis 49:167-185
  fulmineus 49:167-185
Cryptantha
  cinerea ***arenicola*** 46:254-260
  compacta 28:195-198
  creutzfeldtii 42:203-204
  johnstonii 28:195-198
  ochroleuca 28:195-198
  shackletteana 29:28-30
  welshii 42:196-198
Cryptobranchoidea, hyobranchial apparatus 49:482-490
Cryptocarenus
  pubescens 46:265-273
  spatulatus 46:265-273
Cryptogamic soil crusts
  Algae, Uintah Basin, Utah 45:432-442
  Camp Floyd State Park, Utah 46:632-640
  Grazing timing effects
    Great Basin low-shrub desert 49:104-107
  Navajo National Monument, Arizona 43:73-78
  Seasonal algal variation
    Tintic Mountains, Utah 45:14-21
  Trampling disturbance and recovery
    Grand Canyon National Park, Arizona 50:321-325
Cryptops ***calinus*** 17:30-41
Crystal Ball Cave, Utah
  Quaternary paleontology and paleoecology 45:337-390
Ctenosaura
  hemilopha macrolopha 32:104-111
  hemilopha nolascensis 32:104-111
Cui-ui, life history, Pyramid Lake, Nevada 45:571-603
Cupressus arizonica, succession 40:254-264
Curlew, Long-billed
  Diet, Western Idaho 45:85-86
  Habitat comparisons, Wyoming 47:459-466
  Nesting biology 32:88-90
Curlew Valley, Utah, raptors, nesting 31:51-65
Curry County, Oregon
  Aneides ferreus, food habits 46:228-240
Cuterebra
  Larvae, parasitizing *Peromyscus* species 38:51-54
  tenebrosa, field behavior and seasonal activity, Central Washington 34:247-253
Cygnus buccinator, Pleistocene, Utah 46:547-548
Cymopterus
  acaulis ***parvus*** 46:66-106
  higginsii 35:377-378
Cynomys
  Colony attributes, associated vertebrates 42:572-582
  leucurus
    Burrow structure and function 49:517-524
    Diggings in *Pogonomyrmex occidentalis* mounds, Utah 49:36-37
    Hutton Lake National Wildlife Refuge, Wyoming 31:115-124
  ludovicianus
    Ecology, associated species, Western South Dakota 50:339-345
    Livestock grazing 46:198-203
    Mound architecture 49:621-623

    - Populations one year after rodenticides 50:107-113
    - Reproductive ecology, Montana 47:202-206
    - Rodenticide-treated site reoccupation 47:339-343
- *Cynthia*, rare aberrant forms, Utah 31:256-260
- Cyprinidae, *Gila*, systematics, Nevada 10:31-36
- *Cyprinodon*
  - *atrorus*
    - Behavior in differing environments 29:169-180
  - *diabolis*, movement, Devil's Hole, Nevada 43:592-596
  - *nevadensis*
    - Systematics, Ash Meadows, Nevada 46:220-223
  - *salinus*, adapting to fresh water 41:341-342
- *Cyprinus carpio*
  - Diel behavior, Utah Lake, Utah 44:509-515
- *Cyrtopogon* ***albifacies*** 3:1-4
- *Cysteochila*
  - ***aei*** 23:149-158
  - ***apheles*** 23:149-158
  - ***cybele*** 23:149-158
  - ***epelys*** 23:149-158
  - ***incolana*** 16:18-22
  - ***malayana*** 16:18-22
  - ***pelates*** 23:149-158
  - ***vadosa*** 16:18-22

D

- 2,4-D
  - Long-term effects on *Populus tremuloides* 44:459-467
- Dace, Nevadan relict
  - Temperature and salinity relationships 42:541-548
- *Dactylipalpus* ***unctus*** 21:8-9
- ***Daihinibaenetes*** (Orthoptera) 22:12-29
  - ***giganteus*** 22:12-29
  - ***tanneri*** 22:12-29
- ***Dalea epica*** 31:90-92
- Death Valley, California
  - Herpetofauna 23:119-128
  - Pacific tree frog, albino 29:111
- Deer
  - Mule
    - Antelope bitterbrush consumption, summer 44:572-574
    - Bed characteristics 46:542-546
    - Consumption of fresh alfalfa hay 47:100-102
    - Diet similarity with elk, Utah 49:552-555
    - Differential habitat utilization by sexes 40:273-281
    - Fawns, bottle feeding 46:217-219
    - Fecal pellet similarities to pronghorn 38:222-224
    - Fetal growth rates 46:245-248
    - Food preference, *Kochia* accessions 45:778-783
    - Male-female winter mortality in Utah 44:450-452
    - Maxillary canine teeth 43:445-446
    - Occurrence of ticks on, Central Utah 37:407-409
    - Passage beneath overland coal conveyer 44:499-504
    - Pellet-group data and winter range 41:213-220
    - Predator control, Utah 37:101-102
    - Reproduction and plant chemical composition 39:122-128
    - Rocky Mountain, captive behavior 47:105-109
    - Utah, changes in size 49:31-35
    - Wintering, big sagebrush preference 46:281-286
  - White-tailed, Nevada 28:199
- Deer Creek Reservoir, Utah
  - Yellow perch, parasites 31:169-176
- Deer hunters, Utah
  - Responses to checking station questionnaire 49:159-166.
- ***Deladenus obesus*** 2:37-85
- *Dendragapus*
  - *obscurus*
    - Effects of summer weather on harvest 42:91-95
    - Hatching chronology, Northeastern Oregon 46:745-748
    - Microhabitat, Southeastern Idaho 46:117-122
    - Winter habitats and foods, Sheeprock Mountains, Utah 49:229-232
  - *obscurus pallidus*, fall feeding habits 46:123-127
- *Dendrocranulus*
  - ***auctus*** 39:133-142
  - ***gracilis*** 42:223-231
  - ***limbellus*** 39:133-142
  - ***limitaris*** 39:133-142
  - ***mexicanus*** 46:265-273
  - ***modus*** 39:133-142
  - ***pinguis*** 39:133-142
  - ***sobrinus*** 44:113-119
- *Dendroctonus*
  - ***aztecus*** 23:1-117
  - *pseudotsugae*
    - Broods on spruce budworm defoliated trees 48:348-351
    - Emergence, attack densities, hosts, Northern Colorado 50:333-338
  - Systematics, keys 23:1-117
  - ***vitei*** 34:277-290
- *Dendrosinus* ***mexicanus*** 43:647-659
- *Dendroterus*
  - ***confinis*** 19:1-7
  - ***decipiens*** 19:1-7
  - ***fossifrons*** 44:113-119
  - ***modicus*** 44:113-119
  - ***mundus*** 19:1-7
  - ***texanus*** 19:1-7
- Denitrification rates, spring
  - Sierra Nevada plant communities 48:558-562
- *Dentostomella translucida*
  - Morphology in Mongolian gerbils 48:206-215
- *Dermacentor*
  - *albipictus*
    - Occurrence on mule deer, Central Utah 37:407-409
  - *andersoni*
    - National forest sites, Utah 28:30-43
  - *parumapertus*
    - Oviposition and egg development 17:42-51
- Detrital processing, invertebrate
  - Effects of suspended sediments 46:33-38

Devil's Hole, Nevada
  Cyprinodon diabolis movement 43:592-596
Diamond Pond, Harney County, Oregon
  Vegetation history 47:427-458
Diatoms
  Centric, Lake Tahoe 44:83-98
  Cowboy Hot Spring, Mono County, California 46:612-624
  Epiphytic, on *Phragmites australis* 40:223-228
  Floristics and succession, Utah 39:15-43
  Middle Fork Salmon River, Idaho 44:421-427
  Mint Creek, Idaho, checklist 49:155-158
  Northeastern Utah 44:36-48
  Systematics, checklist
    Oregon Caves National Monument 41:317-332
Dicolecia ***serrata*** 48:232-249
Diconocoris ***distanti*** 14:1-10
Dicranoclista ***fasciata*** 19:67-74
Dicranota
  bernardinensis 26:1-8
  diacantha 28:113-123
  lassenensis 24:19-25
  nooksackensis ***brevispinosa*** 18:31-36
  nooksackiae ***latistyla*** 18:31-36
  rainierensis 28:113-123
  sanctaeluciae 24:117-122
Dicrotingis (Tingidae) 20:29-38
Dictyla
  litotes 24:83-92
  poecilla 24:83-92
Dictyotingis ***monticula*** 16:18-22
Digestibility, in vitro, *Kochia prostrata* 44:296-298
Dinosaur National Monument
  Sympatric fishes 50:257-264
Dinosaurs
  Sauropod, Upper Jurassic
    Western Colorado 45:697-709
  Uncompahgre fauna, Western Colorado 45:710-720
  Upper Jurassic, Colorado Plateau 48:121-145
Diphyllobothrium cordiceps larvae
  Parasitizing cutthroat trout, Yellowstone Park 44:125-133
Diplocardia
  texensis 27:1-10
  verrucosa 27:1-10
Diploplectron brunneipes, nest and larva 35:123-125
Diplopods, strawberry damage, Provo, Utah 9:23
Diplostomatosis, infection in Utah fishes 38:473-477
Diplostomum spathaceum
  Life cycle, Utah 36:86-96
  Parasitizing Utah fishes 38:473-477
  Upper Salmon River, Obsidian, Idaho 43:675-683
Diplotaxis
  acononicus 1:127-137
  aequalis 1:127-137
  aulacochela 1:127-137
  brevicornis 1:127-137
  fulgida 1:127-137
  impressifrons 1:127-137
  microps 1:127-137
  parkeri 1:127-137
  persisae 1:127-137
  recticanthus 1:127-137
  saylori 1:127-137
  ungulatus 1:127-137
Dipodomys
  deserti, opportunistic foraging 49:396-397
  merriami, burrowing habits
    Dixie State Park, Utah 31:190-192
    Panamint Valley, California 31:190-192
  microps occidentalis
    Burrows at the Nevada Test Site 24:93-101
  ordii
    Temporal activity patterns 40:282-286
  ordii columbianus
    Histological study of the ovary 1:63-74
  ordii pallidus
    Growth rates 38:215-221
Diptera
  Asilidae, systematics, keys, Utah 47:38-90
  Basilia, systematics, Venezuela 37:221-224
  Bibiocephala, systematics, Idaho 25:1-3
  Bombyliidae
    Systematics, Great Basin 13:17-27
    Systematics, North America 19:67-74
  Bombylius, systematics, keys, Utah 35:407-418
  Clinohelea
    Systematics, keys, Nearctic Region 35:275-287
  Culicidae, Colorado, checklist 9:65-75
  Cyrtopogon, systematics, Utah 3:1-4
  Dolichopodidae
    Systematics, California and Utah 11:11-17
  Ephydridae, systematics, keys 35:65-85
  Exoprosopa
    Systematics, Western United States 18:69-84
  Lordotus, systematics 19:9-26
  Mallophora
    Systematics, Great Salt Lake Desert 18:41-42
  Nycteribiidae, systematics 24:107-115
  Poecilanthrax, systematics, keys 17:1-26
  Rhopalomyia, systematics, North America 37:426-428
  Simuliidae, systematics, keys, Utah 20:81-104
  Tingidae, Nevada Test Site 26:9-16
  Tipula, systematics, Nearctic Region 23:159-165
  Tipulidae
    Systematics, California 24:19-25; 24:117-122
    Systematics, Middle America 30:232-241
    Systematics, Nearctic Region 21:79-86; 25:49-53; 26:1-8; 28:113-123; 28:16-23; 29:1-10; 33:189-196
    Systematics, United States 22:1-7
    Systematics, Western Nearctic Region 4:89-100; 5:93-103; 18:31-36; 21:10-16
Discolaimium
  gigas 10:45-50
  pseudoporum 10:45-50
Distichilis spicata invasion

  Mono Lake, California 45:542-545
Dixidesmus ***phanus*** 11:27-35
Dixie State Park, Utah
  Dipodomys merriami, burrowing habits 31:190-192
Docalidia
  caterva 46:749-762
  convexa 46:749-762
  gracilitas 46:749-762
  paracrista 46:749-762
  pennyi 46:749-762
  setacea 46:749-762
  triquetra 46:749-762
  vella 46:749-762
  vesica 46:749-762
  zanoli 46:749-762
Dogs
  Hydatid disease, field diagnosis 47:207-219
  Sheep, cestode infections, Central Utah 46:208-216
Dona Ana County, New Mexico
  Uta stansburiana stejnegeri 33:124-128
Doroneuria ***baumanni*** 34:83-93
Dorytomus ***rubidus*** 1:31-32
Doves, Mourning
  Use of man-made ponds, Idaho 49:627-631
Draba
  kassii 46:261-264
  Systematics 43:441-444
Dragonflies, termites as food, Provo, Utah 7:29
Drosophila pseudoobscura
  Experimental release, Bryce Canyon 47:32-37
Dryadophis 33:276
Dryosaurus altus
  Small bones, Upper Jurassic, Colorado 33:129-132
Duchesne County, Utah, algal populations
  Bottle Hollow Reservoir 42:205-218
Ducks, Gadwall and Northern Shoveler
  Time-activity budgets, Central Utah 48:280-284
Dugway, Utah, mites 13:35-42
Dulinius ***congruus*** 13:91-99
Dystylosaurus edwini 45:697-709

E

Eagles, Bald
  Snake River Canyon, Wyoming 41:461-464
Earthworms
  Deserts, United States 27:142-176
  Diplocardia, Systematics 27:1-10
Echinocereus engelmannii and *triglochidiatus*
  Ecomorphology, Southeastern California 42:353-359
Echinococcus granulosus
  Field diagnosis in dogs 47:207-219
  Prevalence, sheep dogs, Central Utah 42:65-66
Ecology
  Plant, understory and open-area differentiation 40:167-174
  Regulated stream, Huntington River, Utah 44:231-256
Ectoparasites
  National Reactor Testing Station, Idaho 31:77-82
  Oregon, from mammals 24:75-81
Ectopic limbs, *Hyla regilla* 44:166-169
Edaphic relations
  Southeastern Idaho wildlands 44:265-271
Eimeria
  Infecting Wyoming ground squirrels and white-tailed prairie dogs, Wyoming 50:327-331
Elaeophora schneideri in mule deer
  Central Utah 42:351-352
Elaphrus ***torreyensis*** 2:137-138
Electrophoresis, isoenzymes of western shrubs 41:377-388
Eleodes
  inyoensis 21:55-78
  leechi 21:55-78
Elgaria, significance of scale characters 34:257-266
Elk
  Consumption of fresh alfalfa hay 47:100-102
  Diet similarity with mule deer, Utah 49:552-555
  Unusual tooth wear
    Glacier National Park, Montana 41:368-369
Elm, Siberian, Utah, naturalization 24:103-106
Elymus
  cinereus, insect parasites, Southern Idaho 47:644-651
  simplex, systematics 36:239-241
Engelhardt, George Paul 3:57-58
Enoclerus eximius ***trullionis*** 7:21-22
Eocene, fossil plant ultrastructure, India 41:161-166
Ephemeroptera
  Leptophlebiidae, systematics 47:283-286
  Southeastern Idaho, checklist 38:55-58
Ephydatia mulleri
  Water quality relationships, Idaho 45:391-394
Epilachna varivestis, damage in Utah, 1943 4:61
Epiphyseal fusion
  Rocky Mountain bighorn sheep 47:7-12
Equisetum, SEM stem analysis, Utah 48:51-57
Eremaeus ***stiktos*** 22:89-92
Eremopedes ***kelsoensis*** 32:223-228
Eridiphas slevini ***marcosensis*** 38:406-410
Erigeron
  awapensis 43:365-368
  canaani 43:365-368
  carringtonae 43:365-368
  cavernensis 48:495-498
  goodrichii 43:365-368
  maguirei ***harrisonii*** 43:365-368
  Systematics, Utah 43:365-368
  untermannii 43:365-368
  wahwahensis 43:365-368
  zothecinus 46:261-264
Eriogonum
  atrorubens ***auritulum*** 36:281-333
  atrorubens ***nemorosum*** 36:281-333
  brevicaule ***atwoodii*** 34:245-246
  brevicaule ***promiscuum*** 44:519-557
  clivosum 36:281-333

corymbosum, ecology, Uinta Basin, Utah 39:177-191
corymbosum ***albogilvum*** 27:183-229
corymbosum ***davidsei*** 27:183-229
corymbosum ***velutinum*** 27:183-229
divaricatum 41:143-146
duchesnense 27:183-229
fimbriatum 36:281-333
hylophilum 27:183-229
lancifolium 27:183-229
lewisii 45:276-280
natum 35:327-376
ochrocephalum ***alexanderae*** 45:276-280
ovalifolium ***caelestinum*** 32:113-116
pauciflorum 27:102-117
pelinophilum 33:120-122
pharnaceoides ***cervinum*** 34:245-246
revealianum 30:16-22
saurinum 27:183-229
smithii 27:183-229
soredium 41:229-231
tiehmii 45:276-280
Type specimens, Nevada 45:488-492
umbellatum ***deserticum*** 35:327-376
umbellatum ***devestivum*** 32:113-116
umbellatum ***furcosum*** 45:276-280
umbellatum ***juniporinum*** 45:276-280
umbellatum ***vernum*** 28:157-159
viscanum 36:281-333
Erioptera
chaetophora 28:16-23
melanderiana 5:93-103
platymera 28:16-23
Ermine, Western Utah 28:47
Ernocladius (Scolytidae) 40:89-97
Erysimum asperum purshii 32:221-222
Escalante, Silvestre Valez de
Recognition of ancient Great Basin lakes 22:87-88
Eschatomoxys ***tanneri*** 19:63-66
Esox lucius
Green River Basin, Colorado and Utah 50:33-40
Esterase variation, *Mimulus glabratus* 36:81-85
Ethopolys
calibius 11:115-118
spectans 11:115-118
timpius 11:115-118
Eucyllus ***tinkhami*** 19:53-55
Euderma maculatum
Notes from Southwest Utah 34:254-256
Roosting behavior, Utah 35:121-122
Eumeces
brevirostris ***bilineatus*** 18:57-62
capito, systematics 35:109-112
lynxe ***durangoensis*** 18:57-62
multilineatus 17:111-117
septentrionalis
Bibliography and subject index 49:525-534
Influence of substrate water content on neonate size 49:198-200
Maternal care of neonates 47:536-537
Reproduction, Nebraska 47:373-374
skiltonianus
Ecology, systematics 17:59-94
skiltonianus ***interparietalis*** 17:59-94
skiltonianus skiltonianus, life history, Utah 4:81-88
skiltonianus ***utahensis*** 17:59-94
Systematics, keys 17:59-94
xanthi, systematics 35:109-112
Eupagiocerus
clarus 25:31-35
serratus 21:87-107
vastus 25:31-35
Eupagoderes
hardyi 1:31-32
utahensis 1:31-32
Eupterotegaeus ***rhamphosus*** 28:179-182
European journals, non-receipt, WWII 1:92
Europiella
basicornis 30:227-231
knowltoni 30:227-231
monticola 30:227-231
multipunctipes 30:227-231
Euschistus variolarius
Predation on *Gastroidea cyanea* 14:27-29
Euschongastia
fasolla 15:1-26
lanceolata 15:1-26
lanei 15:1-26
obesa 15:1-26
rotunda 15:1-26
utahensis 15:1-26
Eutamias dorsalis
Genetic variation, Western Utah 47:551-561
Evansolidia
bifurcata 48:232-249
digitula 48:232-249
massa 48:232-249
Exochocepheus eremitus 28:144-146
Exoprosopa
arenicola 18:69-84
butleri 18:69-84
cingulata 18:69-84
doris 18:69-84
sharonae 18:69-84
utahensis 18:69-84

F

Fabaceae
Oxytropis, systematics, Columbia Basin, Washington 50:373-377
Systematics, keys, Utah 38:225-367
Fagaceae, *Quercus*, systematics, keys, Utah 46:107-111
Falco peregrinus anatum
Nesting habitat physiography, Utah 49:408-418
Falcons
Peregrine
Nesting habitat physiography, Utah 49:408-418

  Prairie, flight pattern 25:48
Fall, Henry Clinton 1:62
Farmington Bay, Utah, *Typha latifolia* decline 37:24-34
Faunistic inventory, Nevada Test Site 28:132-141
Felis concolor
  Food, Cascade Range, Oregon 45:77-80
  Winter food habits, Oregon 43:425-428
Fens, California Coast, hydrology 37:57-66
Ferocactus acanthodes
  Slope preference in Southwestern Utah 44:133-139
Ferrets, black-footed, distribution, Wyoming 41:360-361
Fescue, climate and ecology
  Western United States 39:284-288
Fir
  California white, formation of *Pisolithus tinctorius* on, Sierra Nevada 50:85-87
  Douglas
    Dendroctonus pseudotsugae broods on 48:348-351
    Dwarf mistletoe infection, Southwestern United States 46:528-534
    Effects of dwarf mistletoe, Southwestern United States 50:173-179
    Growth variation, Central Utah 39:219-225
    Rhabdocline needle blight 41:476-477
    Site potential, Southwestern habitat types 46:277-280
  Pacific silver
    Douglas-fir dwarf mistletoe, Northern California 47:161-162
  White
    Growth variation, Central Utah 39:219-225
Fishes
  Exotic, Idaho and Wyoming 47:523-526
  Feeding interrelations
    Aravaipa Creek, Arizona 41:409-426
  Introduced, status in Southern Nevada 42:361-366
  Native, life history
    Alvord Basin, Oregon-Nevada 43:409-420
  Nongame insectivorous
    Food habits in Oklahoma 45:721-733
  Populations, impact of cattle on
    Pahranagat Valley, Nevada 49:491-495
  Species composition and abundance
    Pyramid Lake, Nevada 41:395-408
  Thermal tolerances, Virgin River 47:538-546
  Threatened, Warner Basin, Oregon 50:243-248
  Vertical distribution
    Pyramid Lake, Nevada 38:417-428
Fish hatchery history, Utah and Nevada 46:583-594
Fish Springs, Utah, Mollusca 31:223-236
Fistulidia simplex 48:232-249
Flaming Gorge Reservoir, Utah
  Kokanee reproductive characteristics 48:46-50
Flea-host associations, Utah 12:67-75
Fleas
  Exchange between deer mice and rodents, Western Utah 36:475-480
  Host and distributional records, Utah 26:71-75
  Host relationships and range
    Western United States 45:530-532
  National Reactor Testing Station, Idaho 28:73-87
  Plague in pine martens 44:170-175
Fleming, John
  Contributions to herpetological nomenclature, 1822 32:55-60
Flies
  Deer, vectors of tularemia, Utah Lake, Utah 25:13-29
  Preying on mosquitoes, Utah and Wyoming 9:21-23
Flint Creek, Oklahoma
  Nongame insectivorous fish, food habits 45:721-733
Flora
  Alaska, nomenclature changes 28:147-156
  Alpine vascular
    Teton Range, Wyoming 41:232-242
    West Elk Mountains, Colorado, checklist 47:152-160
  Orange Cliffs, Utah, checklist 47:287-298
  Pine Butte Fen, Montana 46:22-32
  Rare, Colorado 48:434-484
  Southwest, annotated bibliography 42:105-112
  Stansbury Moutains, Utah, checklist 43:619-646
  Utah
    Desert and mountain comparative studies 43:385-393
    Miscellaneous families, systematics, keys 40:38-58
  Vascular
    Bryce Canyon National Park, Utah, checklist 48:352
    Wyoming 44:482-483
Floristic analysis, Southwestern United States 46:46-65
Flowers, Seville 44:210-222
Flukes, eye
  Parasitizing Utah fishes 38:473-477
  Upper Salmon River, near Obsidian, Idaho 43:675-683
Forbs, seed viability, long-term storage 41:274-277
Forests
  Montane, biomass
    Mogollon Plateau, Arizona 44:627-634
  Riverbottom, Alberta, Canada 36:243-271
Formica
  obscuripes, flights of, Nevada 32:202-207
  propinqua, nests, Nevada 41:389-392
FORTRAN IV computer programs
  Meteorologic measurements, Central Utah 35:203-230
Fossil Butte National Monument, Wyoming
  Mammals, preliminary survey 37:91-94
Foxes
  Kit, arthropod consorts 20:71-77
  Red
    Diets when sympatric with coyotes 41:251-254
    Intercanine crown distances, South Dakota 42:601-602
  Swift, denning, diet, Western South Dakota 46:249-253
Frogs
  Arizona tree, calls 46:378-381

Arizona-Sonoran Desert
Sexual selection and mating 45:688-696
Pacific tree, albino
Death Valley, California 29:111
Ribbed, nomenclatural problems
New Zealand and American 31:261-264
Western spotted, ecology and life history 29:45-81
Fungi
Native pine stem rust
Phalacropsis dispar, a natural control 42:369-379
Soil, between and beneath pinyon-juniper canopies, New Mexico 50:167-172
Fusichila waipaheenas 13:75-85

G

Galium emeryense 37:510
Galls, tephritid
Specificity on *Chrysothamnus nauseosus* 39:81-87
Gastroidea cyanea
Predation by *Euschistus variolarius* 14:27-29
Gentianaceae
Centaurium, systematics, Great Basin 41:192-197
Systematics, keys, Utah 36:483-495
Geophilus ***becki*** 11:27-35
Geraniaceae
Geranium
richardsonii, systematics 29:25-27
Systematics, keys, Utah 34:297-304
Geranium
richardsonii 29:25-27
Systematics, keys, Utah 34:297-304
Gerrhonotus, significance of scale characters 34:257-266
Gila
atraria, Pleistocene, Corrine, Utah 49:131-133
bicolor
Biology, Walker Lake, Nevada 42:60-64; 45:784-788
Reproductive biology, Pyramid Lake, Nevada 38:203-207
Seasonal growth, Pyramid Lake, Nevada 43:713-716
bicolor euchila, status and distribution 46:441-444
boraxobius, feeding ecology, Oregon 40:101-114
cypha, Yampa and Green rivers, Utah 50:257-264
jordani 10:31-36
robusta, Yampa and Green rivers, Utah 50:257-264
Gilia tenuis 49:461-465
Glacier National Park, Montana
Unusual tooth wear in elk 41:368-369
Vegetational and geomorphic change
Avalanche paths 45:313-317
Glaux maritima
Habitat relationships in Central Utah 44:299-309
Gnatharus tibetensis 46:461-464
Gnathophthorus ***clematus*** 35:391-401
Gnathotrichus
alniphagus 44:113-119
dentatus 27:36-57
imitans 27:36-57
nimifrons 27:36-57
perniciosus 27:36-57
Gnathotrupes
colaphus 49:167-185
nectandrae 49:167-185
Gnathotrypanus (Coleoptera) 28:1-15
electus 28:1-15
terebratus 28:1-15
Gonomyia
flintiana 21:10-16
leechi 24:19-25
lindseyi 5:93-103
persimplex 29:1-10
Gopher mounds, revegetation in Utah 34:267-275
Gophers, pocket, spruce-fir forest, Idaho 41:362-367
Gopherus agassizi, courtship behavior 36:467-470
Goshen, Utah, salt playa vegetation 39:44-58
Goshen Ponds, Utah, diatom flora, 38:211-214
Gracilidia gracilis 48:232-249
Grackle, Great-tailed
Nesting record, Nevada 45:483-484
Grand Canyon National Park, Arizona
Cryptogamic soil crusts, trampling disturbance and recovery 50:321-325
Grand Teton National Park, Wyoming
Bee visitors of sweetvetch 47:314-318
Microtines
Distribution, interspecies interaction 33:205-217
Mosses, checklist 45:124-126
Grant County, Oregon, herpetology 30:9-12
Grass Lake, California
Ambystoma, relictual population 38:429-437
Grasses, New Mexico
Bibliography of taxonomy and types 50:73-82
Grasslands
Arid, soil texture and species diversity
Eastern Great Basin 33:163-168
Fescue, climate in Western United States 39:284-288
Grazing
Differential effects, cattle and sheep
Central Utah 45:141-149
Impact on natural springs
South Central Nevada 50:289-294
Timing, effect on cryptogamic communities, Great Basin low-shrub desert 49:104-107
Greasewood, germination factors 47:110-116
Great Basin
Butterflies, zoogeography 47:186-201
Conifers 31:85-89
Desert heteromyid community
Competition for food and space 47:1-6
Desert, Eastern
Nest site selection in raptor communities 42:395-404
Grazing and passerine breeding birds 46:567-572
Herpetological studies 24:37-57

  - Late Pleistocene fauna
    - Snake Creek Burial Cave 49:143-154
  - Low-shrub desert
    - Timing effect of grazing 49:104-107
  - Monoterpene concentrations
    - Pinyon litter, soil 48:228-231
  - Natural history, 1800-1855 1:33-61
  - Pinyon-juniper woodlands
    - Succession following wildfire 45:556-566
  - Plant-soil relationships
    - Hydrothermally altered areas 43:457-469
  - Red-necked Phalaropes
    - Migration biology 46:185-197
  - Reptiles in BYU and U. of U. collections 26:87-135
  - Rodent fauna, niche pattern 47:488-496
  - Tularemia 39:103-121
  - Understory response
    - Pinyon-juniper harvesting 45:105-112
  - Vertebrate communities
    - Influence of vegetation 46:711-720
- Great Basin, Eastern
  - Soil texture, arid grassland species diversity 33:163-168
- Great Basin, Northern
  - Rodents, annual energy budgets 39:143-154
  - *Sorex preblei*, distribution 50:93-95
  - Turkeys, postglacial 31:48-49
- Great Basin, Western
  - Nectar-sugar concentrations and flower visitors 37:523-529
- Great Basin Naturalist, cover design 14:38
- Great Plains, Northern
  - Water impoundments
    - Waterfowl and shorebird use 48:353-357
- Great Salt Lake, Utah
  - Biological investigations, summary 34:221-229
  - Birds, checklist 37:247-251
  - California Gull, nesting populations 50:299-302
  - Insular biogeography of mammals 42:589-596
  - Nesting waterfowl
    - Response to wetland flooding 49:614-617
  - Use of water for lobster culture 39:231-240
- Great Salt Lake Desert, Utah
  - Sucking lice, keys 16:9-17
- Grebe, Clark's
  - Breeding records, Colorado and Nevada 46:581-582
- Green River Basin, Colorado and Utah
  - *Esox lucius* and *Stizostedion vitreum* 50:33-40
- Green River Formation, Utah, fossil turtle 30:13-15
- Greer County, Oklahoma, amphibians 15:27-31
- Grimmiaceae
  - Nevada, checklist, distribution 42:583-588
- Grouse
  - Blue
    - Effects of summer weather on harvest 42:91-95
    - Feeding habits, early fall 46:123-127
    - Hatching chronology, Northeastern Oregon 46:745-748
    - Microhabitat, Southeastern Idaho 46:117-122
    - Winter habitats and foods, Sheeprock Mountains, Utah 49:229-232
  - Sage
    - Big sagebrush, selection 48:274-279
    - Comparison with Sharp-tailed Grouse leks, Wyoming 49:275-278
    - Habitat use by breeding males 49:404-407
  - Sharp-tailed
    - Comparison with Sage Grouse leks, Wyoming 49:275-278
- Gulls
  - California
    - Banding, Utah Lake 2:98; 3:55-57; 8:37-39
    - Comparative plumage 4:57-61
    - Life history, Utah Lake 3:91-108
    - Nesting colonies, Wyoming 46:128-133
    - Populations nesting at Great Salt Lake, Utah 50:299-302
  - Franklin's, history and status
    - Malheur National Wildlife Refuge 41:440-444
  - Herring, occurrence of at Utah Lake 3:54
- *Gutierrezia sarothrae* ***pomariensis*** 30:16-22
- *Gymnodamaeus*
  - ***chalazionus*** 32:97-103
  - ***leurolomasus*** 33:37-42
  - ***plokosus*** 33:37-42
  - ***veriornatus*** 21:27-28
- *Gyromitra*
  - *fastigiata*, Utah 31:35-47
  - *gigas*, Utah 31:35-47

H

- *Habenaria* ***zothecina*** 46:254-260
- Habitat
  - Winter use patterns of elk, mule deer and moose, Wyoming 47:538-643
- ***Hadrodemius*** (Scolytidae) 40:89-97
- *Haedus*
  - ***cirratus*** 24:83-92
  - ***javancus*** 13:91-99
- *Haemonchus contortus*
  - Effect of irrigation on larval survival 38:369-378
- Hagerman Valley, Idaho
  - Shoshone sculpin distribution 44:324-326
- *Haliplus* ***eremicus*** 49:89-91
- Haloxon, efficacy as sheep anthelmintic 29:35-41
- Hanging gardens
  - Utah, distribution, diversity 49:1-30
  - Zion National Park, Utah 40:178-182
    - Dispersal types, flood frequency 40:365-371
- *Haplopappus*
  - ***alpinus*** 40:73-77
  - *armerioides* ***gramineus*** 43:371-372
  - ***crispus*** 43:358-364
  - Systematics, Utah 43:358-364
  - ***zionis*** 43:358-364
- *Harasupia*

- ***austini*** 49:233-240
- ***baja*** 49:233-240
- ***mexicana*** 49:233-240
- ***retrorsa*** 49:233-240
- ***ungula*** 49:233-240

Hatcheries, fish, history, Utah and Nevada 46:583-594

Hawks
- Ferruginous
  - Ground nesting, West Central Utah 28:111
  - Population dynamics, West Central Utah 37:411-425
- Night, distribution, Utah 1:93-96
- Swainson's
  - Central Utah, feeding and behavior 46:302-304
  - Ground nesting, aggressive behavior 39:253-254

Hayes, Sheldon P.
- Cold-blooded vertebrate collection 3:59

Hebrus ***amnicus*** 13:9-11

Hedysarum
- *boreale*
  - Nodulation, acetylene reduction, Great Basin 44:151-158
  - Systematics 36:458-460
- *boreale boreale*, bee pollen-collecting 47:314-318
- *occidentale* ***canone*** 38:225-367
- Systematics, keys 30:109-130

Hells Canyon, birds, checklist 49:279-287

Helminths
- Cat and dog parasites, Central Utah 36:471-474
- Mink parasites, Southwestern Montana 33:53-60
- *Sceloporus* lizard parasites, Utah 33:1-18
- Utah Valley, Utah 30:131-145

Helobdella stagnalis
- Colorado River, Colorado 44:361-362

Hemiptera
- *Ambrysus*, systematics, Venezuela 30:1-4
- *Anommatocoris*, systematics, Panama 22:8-11
- Aquatic and semiaquatic
  - Southwestern United States 33:113-119
- *Hebrus*, systematics 13:9-11
- *Hydrometra*, systematics, Peru 14:61-66
- Hydrometridae
  - Systematics, checklist, Neotropical Region 19:43-52
  - Systematics, Venezuela 12:47-54
- *Microvelia*, systematics, keys, Americas 34:207-217
- Miridae
  - Systematics, Western United States 30:227-231
- Neididae, Nevada Test Site 26:9-16
- Pentatomidae, Nevada Test Site 26:9-16
- Saldidae
  - Stridulatory organs 11:43-46
  - Systematics, Mexico 32:137-153
  - Systematics, North America 10:51-61
- Systematics, Grand Canyon 36:221-226
- Tingidae
  - Africa and Asia 16:18-22
  - Systematics 13:13-16; 13:91-99; 14:1-10; 20:29-38; 29:129-132
  - Systematics, Dominica 28:161-171
  - Systematics, Eastern Hemisphere 23:149-158
  - Systematics, Ethiopia 24:83-92
  - Systematics, India 21:108-113; 24:27-30
- *Trepobates*, systematics 12:35-38
- Veliidae
  - Systematics, Neotropical Region 11:37-42
  - Systematics, Venezuela 12:47-54

Hemoglobin variation
- *Peromyscus maniculatus* 39:192-194

Henderson, William Williams 5:23-24

Henry Mountains, Utah
- Wahweap milkvetch, population cycles, seed reserves 48:541-547

Heron, Great Blue
- Found dead at 11,000 feet, Utah 32:112

Herpetological specimens
- BYU vertebrate collection 1:138-146

Herpetological studies
- Great Basin, United States 24:37-57

Herpetology
- Baker County, Oregon 18:63-65
- Grant County, Oregon 30:9-12
- Hawaii and Western North America
  - Distribution and life history notes 30:106-107
- Malheur County, Oregon 9:59-63
- Pacific Islands
  - Admiralty Islands 11:1-10
  - Australia 12:1-12
  - Guadalcanal 11:53-86
  - Korea 13:67-73
  - Malay 13:1-7
  - Mariana Islands 9:1-20
  - Marquesas Islands 12:1-12
  - Morotai Island 10:1-30
  - New Guinea 12:1-12
  - Philippine Islands 9:25-39
  - Solomon Islands 11:53-86
  - Tahiti 12:1-12

Hesperoperla ***hoguei*** 40:63-67

Hesperophylax occidentalis, detrital processing 46:33-38

Hesperotettix, systematics
- Corrections 6:126
- Utah 3:9-21

Heteromyid community, competition for food, space
- Great Basin Desert 47:1-6

Heteroptera
- Gerridae, systematics, keys, Idaho 49:259-274
- *Lopidea*, systematics
  - Western North America 50:135-154

Heterosphyronida, systematics, New Mexico 12:39-45

Hexacolus
- ***multistriatus*** 21:87-107
- ***obscurus*** 21:87-107
- ***reticulatus*** 21:87-107
- ***tenuis*** 21:87-107

Hexatoma

- ***azrael*** 4:89-100
- ***intrita*** 4:89-100
- ***mariposa*** 4:89-100

Hip glands, montane voles 44:468-470

Holocene, Early
- Coniferous woodlands, Lucerne Valley, California 36:227-238

Homarus americanus
- Culture in Great Salt Lake water 39:231-240
- Growth, semiopen and closed culture systems 42:67-72

Homing, pygmy rabbits 39:88

Homophron
- ***tanneri*** 2:99-104
- *tanneri* ***proximum*** 2:99-104

Homoptera
- Aphidae, systematics, Mt. Timpanogos, Utah 3:5-8
- *Cinara*
  - Systematics, Colorado 21:17-19
  - Systematics, Delaware 21:20-22
  - Systematics, keys, North America 21:35-50
- *Coelidia*, systematics, keys 43:669-674
- Coelidiini
  - Systematics, keys, Neotropical Region 48:232-249
- *Docalidia*
  - Systematics, keys, South America 46:749-762
- *Harasupia*, systematics, keys 49:233-240
- *Paracarinolidia*
  - Systematics, keys, South America 49:92-95
- *Paralidia*, systematics, keys 46:329-335
- *Stenolidia*, systematics, Guyana 46:134-136
- *Stylolidia*, systematics, Malaysia 46:137-139
- Teruliini
  - Systematics, keys 49:398-403
  - Systematics, Neotropical Region 49:96-99
- *Thagria*
  - Systematics, keys, Oriental Region 46:321-328
- *Utamphorophora*
  - Systematics, Mount Timpanogos, Utah 7:1-6

Hoplitophthorus
- ***boliviae*** 21:87-107
- ***cubensis*** 21:87-107
- Spelling correction 21:87-107

Hoplitoplithorus sentus 21:1-7

Hoplopleura
- ***mendezi*** 32:121-136
- ***scotinomydis*** 32:121-136

Host-parasite relationships
- *Dermacentor hunteri* 23:166
- Ectoparasites of mammals, Oregon 24:75-81
- Mites
  - Grasshopper mice parasites, Atomic Test Site, Nevada 22:101-104
  - Nevada Test Site 24:71-73
  - *Peromyscus* parasites, Utah 17:95-102
  - Utah 17:95-102
- *Posthodiplostomum minimum* 36:334-346
- Sucking lice, Utah 16:9-17
- Ticks, San Mateo County, California 24:1-6

Hot Creek Spring, Nevada
- White River springfish, foods and feeding 49:249-251

House Range, Utah
- Vascular plant checklist, communities 48:102-116

Huntington River, Utah
- Ecology of a regulated stream 44:231-256

Hurdchila (Tingidae) 13:91-99

Hutchings, John 3:86-90

Hutton Lake National Wildlife Refuge, Wyoming
- Prairie dog burrows 31:115-124

Hybopsis gracilis, biology, Montana 45:332-336

Hydatid disease
- Central Utah 43:65-72
- Dog owner knowledge
  - Sanpete County, Utah 40:216-220

Hydrology, Bear Lake Basin, Utah-Idaho 46:690-705

Hydrometra
- ***alloiona*** 19:43-52
- ***ciliosa*** 19:43-52
- ***crossa*** 19:43-52
- ***exalla*** 19:43-52
- ***fuanucana*** 14:61-66
- ***huallagana*** 14:61-66

Hydroperla crosbyi, life cycle, Texas 37:260-273

Hydrophyllaceae
- *Phacelia*
  - Systematics, keys, North America 35:127-190
- Systematics, keys, Utah 36:1-55

Hydroporus ***transpunctatus*** 2:99-104

Hydrothermally altered areas
- Plant-soil relationships, Great Basin 43:457-469

Hyla
- ***macrotympanum*** 17:52-56
- *regilla*
  - Albino from Death Valley, California 29:111
  - Ectopic limbs 44:166-169
  - *wrightorum*, calls 46:378-381

Hylastes
- ***asperatus*** 35:21-32
- ***mexicanus*** 27:36-57
- ***retifer*** 42:223-231

Hylesinus
- ***aztecus*** 40:353-358
- ***caseariae*** 46:265-273

Hylocurus
- ***atkinsoni*** 47:547-550
- ***clarki*** 39:133-142
- ***crotonis*** 47:547-550
- ***dissimilis*** 44:113-119
- ***femineus*** 19:57-62
- ***longipennis*** 39:133-142
- ***micaceus*** 44:113-119
- ***minor*** 21:1-7
- ***prolatus*** 42:223-231
- ***scitulus*** 44:113-119
- ***secus*** 44:113-119

Hylurdrectonus **corticinus** 40:89-97
Hylurgops **reticulatus** 31:69-76
Hylurgus **indicus** 45:266-275
Hymenoptera
  Aculeata, Nevada, checklist 43:403-408
  Aphaenogaster, systematics 2:118-121
  Formicidae, Western Nevada 11:91-96
  Stenamma, systematics 32:35-39
  Tiphiidae, Nevada Test Site, checklist 33:109-112
Hymenoxys **lapidicola** 43:373-374
Hyobranchial apparatus, Cryptobranchoidea 49:482-490
Hyphoderma **deserticola** 35:288-304
Hypsiglena
  nuchalatus 4:49-54
  ochrorhynchus **deserticola** 5:25-92
  ochrorhynchus **klauberi** 5:25-92
  ochrorhynchus **lorealus** 5:25-92
  ochrorhynchus **tortugaensis** 5:25-92
  ochrorhynchus **unaocularus** 5:25-92
  Reproduction 41:310
  slevini 4:49-54
  torquata
    Idaho distribution 44:313-316; 45:291-292
  torquata **tiburonensis** 41:139-142

I

Idaho
  Anisakid larvae in fishes 45:427-431
  Birds, distribution and breeding 43:717-727
  Cerambycidae, distribution and bionomics 29:88-95
  Clearwater drainage, sculpins
    Morphometry, keys 38:115-122
  Clearwater River Basin, sculpin distribution 39:59-62
  Collembola, checklist 16:1-6
  Exotic fishes 47:523-526
  Fossil chelonians, Upper Pliocene 29:82-87
  Hagerman Valley
    Shoshone sculpin, distribution 44:324-326
  Idaho National Environmental Research Park
    Vertebrate fauna 46:513-527
  Idaho Primitive Area
    Columbian ground squirrels, ecology 40:362-364
    Columbian ground squirrels, seasonal activity 40:175-177
  Lava Tube Caves, bat hibernation 46:241-244
  Mint Creek, diatom flora, checklist 49:155-158
  Mourning Dove use of man-made ponds 49:627-631
  Mugo pine, cone spittlebug 44:338-348
  National Engineering Laboratory
    Coleoptera, checklist 46:287-293
    Rare vascular plants 44:140-144
    Reptile responses to land management 39:255-262
  National Reactor Testing Station
    Ants 31:237-242
    Ectoparasites 31:77-82
    Fleas 28:73-87
    Scorpions 33:251-254
    Small mammals 33:246-250
    Solpugids 31:164-168
    Spiders 29:105-108
  Obsidian
    Diplostomum spathaceum in fishes 43:675-683
  Oreana local fauna (Blancan), bird fossils 46:763-768
  Palisades Creek
    Cutthroat trout food size selection 45:327-331
  Pocket gophers in spruce-fir forest 41:362-367
  Reptiles and amphibians 44:111-112
    Checklist 2:87-97
  River of No Return Wilderness Area
    Coyote summer food habits 50:63-65
    Plant nutrient levels on summer ranges 44:621-626
  Salmon River, Middle Fork
    Diatoms, distribution and abundance 44:421-427
  Scolytidae, checklist 47:375-382
  Water striders, biology, systematics, keys 49:259-274
Idaho, Southeastern
  Blue Grouse 46:117-122
  Burrow diameter, five mammal species 49:646-649
  Burrowing Owls, food habits 39:274-276
  Coyotes, seasonal foods 42:45-49
  Diets of sympatric red foxes and coyotes 41:251-254
  Edaphic relations in wildlands 44:265-271
  Ephemeroptera, checklist 38:55-58
  Kipukas and species numbers 42:113-119
  Plecoptera, checklist 36:501-504
  Sagebrush vole burrows 47:276-279
  Short-horned lizard activity patterns 45:607-614
  Trichoptera, checklist 37:253-257
  Universal soil loss equation 43:579-584
  Vertebrate fauna, radioactive leaching pond 38:64-70
Idaho, Southern
  1900 alien plant invasion 41:176-183
  Herbivorous and parasitic insects
    Great Basin wildrye 47:644-651
Idaho, Southwestern
  Birds, checklist 43:728-738
  Uta stansburiana stansburiana
    Reproduction 43:477-482
Idaho, Western
  Long-billed Curlew, diet 45:85-86
Idaho National Environmental Research Park
  Vertebrate fauna 46:513-527
Idaho Primitive Area, Idaho
  Columbian ground squirrels
    Seasonal activity 40:175-177
    Ecology 40:362-364
Iguanidae
  Comparative osteology and myology
    Head and neck 37:35-56
  Sceloporine evolution and phylogeny 35:1-20
Ilex rushforthii 31:189
India
  Eocene fossil plant ultrastructure 41:161-166
Indocryphalus **machili** 48:196-201
Insects
  Aquatic

    - Composition and abundance, Convict Creek, Sierra Nevada 46:595-611
    - Infection by larval *Paragordius* 29:44
    - Montezuma Well, Arizona 49:85-88
    - Tolerance to low oxygen concentrations 34:45-59
  - Communities, faunas, Northern Utah 45:37-60
  - Community comparisons
    - Burned and unburned areas 46:721-727
  - Nevada Test Site 26:9-16
  - Sylvan Springs, Yellowstone National Park 44:99-103
  - Trapping methods, rangeland 48:383-387
  - Type specimens in BYU collection 29:150-164; 29:183-205; 34:317-322
- Intermountain Region
  - Biogeography of leeches, mollusks, amphibians 46:736-744
- Intermountain West
  - Mosses, checklist 48:394-401
- Invertebrates
  - Caves, Uinta Mountains, Utah, checklist 41:207-212
  - Colorado, alpine lake and stream chain 47:500-511
  - Lava Tube Caves
    - Arizona and New Mexico 42:405-412
- *Iotichthys phlegethontis*, spawning 40:139-140
- Iowa, Kalsow Prairie
  - Mima mound vegetation 42:246-261
  - Plant species, ecology 43:137-167
  - Zonation patterns in potholes 40:372-384
- *Ips*
  - ***orientalis*** 46:461-464
  - *pilifrons* ***thatcheri*** 35:21-32
  - ***sulcifrons*** 20:59-69
  - ***utahensis*** 20:59-69
- *Irbisia pacifica*
  - Feeding behavior, effects on host plants 48:68-74
- *Iris* ***pariensis*** 46:254-260
- Irrigation, effects
  - Survival of *Haemonchus contortus* larvae 38:369-378
- Isoenzymes, electrophoresis, western shrubs 41:377-388
- *Isoperla*
  - ***coushatta*** 36:211-220
  - ***jewetti*** 36:211-220
  - ***sagittata*** 36:211-220
- Isopods, Nevada Test Site 25:43-47
- *Isotoma* ***spatulata*** 4:39-48
- Isozymes, *Atriplex canescens* 46:157-160

J

- Jackrabbits
  - Black-tailed
    - Courtship behavior 33:203-204
    - Fecal production and protein content 42:567-571
    - Home range and activity patterns, Utah 50:249-256
    - *Kochia americana* abundance 44:635-646
  - Disturbance of mammal traps by 22:83-86
  - White-tailed
    - Courtship behavior 33:203-204
    - Helminth parasites, Colorado-Wyoming 45:604-606
- Jackson Hole, Wyoming
  - American marten demographics 49:587-596
  - *Philanthus*, nests and prey 26:35-40
- Jarocki, Felix Pawel
  - Contributions to herpetological nomenclature, 1822 32:55-60
- *Jikradia* ***infula*** 49:398-403
- *Juglans major*
  - Seed production and seedling establishment 50:47-56
- Juncaceae, systematics, keys, Utah 46:366-377
- Junipers
  - Diameter-weight relationships 42:73-76
  - Western, leaf area and biomass estimation 47:349-354
  - Woodlands
    - Decreases in Utah valleys since settlement 39:263-266
- *Juniperus*
  - *occidentalis*, leaf area, biomass estimation 47:349-354
  - *osteosperma*, disease prediction 46:427-440
  - *scopulorum*, diameter-weight relationships 42:73-76
- Jurassic, Late
  - Brachiosauridae, Utah and Colorado 47:592-608
- Jurassic, Upper
  - *Dryosaurus altus*, small bones, Colorado 33:129-132
  - Mammalian humerus, Colorado 43:551-553

K

- Kaiparowits Basin
  - Vascular plants, checklist 38:125-179
  - Vertebrates, checklist, distribution 40:303-350
- Kaiparowits Region, Utah, biotic study 1:97-126
- Kalsow Prairie, Iowa
  - Mima mound vegetation 42:246-261
  - Plant species, ecology 43:137-167
  - Zonation patterns in potholes 40:372-384
- Kane County, Utah
  - Winterfat communities, release from grazing pressure 46:148-156
- Kangaroo rats
  - Burrows at the Nevada Test Site 24:93-101
  - Histological study of the ovary 1:63-74
  - Opportunistic foraging 49:396-397
- Karyotypes, *Artemisia* species 39:419-426
- Kawich Mountains, Nevada
  - Birds of the pinyon association 16:32-33
- Kingbirds, Montana, frequency distribution 3:109-114
- Kings Peak, Uinta Mountains, Utah
  - Alpine plant communities 42:50-59
- Kipukas, species numbers, Southeastern Idaho 42:113-119
- Koch's Die Pflanzenlause
  - Note to commemorate 100th anniversary 14:79-82
- *Kochia*
  - *americana*
    - Livestock, jackrabbit role in abundance 44:635-646

- *prostrata*
  - In vitro digestibility 44:296-298
  - Range use characteristics 45:778-783
- Kokanee, reproductive characteristics
  - Flaming Gorge Reservoir, Utah 48:46-50
- *Korsigianus* ***christopheri*** 49:398-403
- Kramer Palouse Natural Area, Washington 43:421-424

L

- *Lachnus montanus*, alate form, morphology 14:21-22
- *Laelaps*
  - ***acomys*** 36:113-206
  - ***malacomys*** 36:113-206
  - ***myomys*** 36:113-206
  - ***parasimillimus*** 36:113-206
- *Lagopus mutus*
  - Foods and weights, Amchitka, Aleutian Islands, Alaska 48:533-540
- Lake Gilbert, Nevada
  - Plant communities, landforms 46:1-21
- Lake Powell, ecology of beetles 39:89-96
- Lake Tahoe
  - Centric diatoms 44:83-98
  - Ecology and trophic status 47:562-582
- Lamiaceae, *Salvia*, systematics 41:198-200
- *Lampropeltis*
  - *pyromelana*
    - Reproduction 41:314-316
    - Systematics 13:47-66
  - *pyromelana* ***infralabials*** 13:47-66
  - *pyromelana* ***woodini*** 13:47-66
  - *triangulum taylori*, reproduction, Utah 33:202
- Land clearing
  - Effects on winter annuals, Mohave Desert 47:234-238
- Land reclamation
  - Plant survival on coal mine spoils 41:271-273
- Land survey notes
  - Using to reconstruct presettlement landscapes, American West 50:181-191
- LANDSAT satellite imagery
  - Mule deer population trends 41:213-220
- ***Lanonyx lanaius*** 13:75-85
- Laramie Basin, Wyoming
  - Richardson's ground squirrel, ecology 30:55-70
- Laramie Basin, Wyoming-Colorado
  - Vegetation, postglacial 43:377-384
- Laramie Plains, Wyoming
  - Thirteen-lined ground squirrels, behavior 41:243-246
- *Larus californicus*
  - Nesting colonies
    - Great Salt Lake, Utah 50:299-302
    - Wyoming 46:128-133
- Las Vegas, New Mexico
  - Amphibians, observations 2:109-117
  - Reptiles 9:55-57
- Lava Tube Caves, Arizona and New Mexico
  - Invertebrates and zoogeographic significance 42:405-412
- Lava Tube Caves, Idaho, bat hibernation 46:241-244
- Leaf area and biomass estimation
  - Non-destructive measures, western juniper 47:349-354
- Leaf cross sections, computer analysis
  - Related to environmental conditions 48:334-347
- Leaf litter decomposition
  - Excluding shredders 46:204-207
- Leaf morphology
  - *Artemisia tridentata* subspecies 35:325-326
- Lee Creek Valley, Alberta
  - Vascular plants, checklist 39:277-283
- Leeches
  - *Apatemon gracilis* penetration 36:97-100
  - Biogeography, Intermountain Region 46:736-744
- Leguminosae
  - *Astragalus*
    - Systematics, Colorado 45:31-33
    - Systematics, Utah 45:551-552
    - Systematics, Utah-Nevada 44:263-264
  - *Hedysarum*
    - Systematics, keys, North America 30:109-130
  - *Oxytropis*, systematics, North America 50:355-360
  - *Psoralea*, systematics, keys 32:76-87
- *Leiolopisma smithi* 31:135-137
- *Lemmiscus curtatus*, burrows, Southeastern Idaho 47:276-279
- *Leperisinus* ***guatemalensis*** 27:79-97
- *Lepidium*
  - *barnebyanum*, new name 27:177-181
  - *montanum* ***neeseae*** 37:279-365
  - *montanum* ***stellae*** 37:279-365
  - ***ostleri*** 40:78-88
- Lepidoptera, Nevada Test Site 29:42
- *Leptodictya* ***archboldi*** 28:161-171
- *Leptopharsa*
  - ***avia*** 13:13-16
  - ***bredini*** 28:161-171
  - ***inannana*** 13:13-16
  - ***milleri*** 14:1-10
  - ***paulana*** 13:13-16
  - ***quadrata*** 14:1-10
  - ***ralla*** 23:149-158
- *Leptosporomyces* ***juniperinus*** 38:42-48
- *Leptotyphlops*
  - *dulcis* ***supraocularus*** 45:615-676
  - *humilis boettgeri*, correct name 34:94-96
  - *humilis* ***chihuahuaensis*** 45:615-676
- ***Leptoxyleborus*** (Scolytidae) 40:89-97
- *Lepus*
  - *californicus*
    - Home range and activity patterns, Utah 50:249-256
  - *californicus deserticola*
    - Fecal production and protein content 42:567-571
  - *townsendi*
    - Helminth parasites, Colorado-Wyoming 45:604-606
- *Lesquerella*

  - *hemiphysaria* **lucens** 37:279-365
  - *hitchcockii* 30:94-98
  - Systematics, keys 30:94-98
- Leucism, Western Bluebird 48:75-77
- *Liacarus* **lectronus** 29:140-142
- Lice, sucking
  - Great Salt Lake Desert, Utah, keys 16:9-17
- *Lichanura*
  - *roseofusca*, systematics 40:59-62
  - *trivirgata* **bostici** 38:411-416
- *Ligula intestinalis*
  - Yellow perch parasite, Deer Creek Reservoir, Utah 31:169-176
- Lily Lake, Utah
  - Aquatic Phycomycetes 32:181-189
  - Diatom floristics and succession 39:15-43
- *Limnephilus*
  - Predation by *Ambystoma tigrinum nebulosum* 43:475-476
- Limnology, Soda Lake, Nevada 31:106-108
- *Limnophila*
  - **boharti** 4:89-100
  - **burdicki** 24:117-122
  - **byersi** 33:189-196
  - **freeborni** 4:89-100
  - **frosti** 21:79-86
  - **modoc** 5:93-103
  - **nearctica** 26:1-8
  - **paeneadusta** 21:79-86
  - **sequoiarum** 4:89-100
  - **vancouverensis** 4:89-100
- *Limonia*
  - **acinomeca** 28:113-123
  - **apiceglabra** 28:113-123
  - *californica* **decreta** 28:113-123
  - **chillcotti** 28:113-123
  - **dreisbachi** 25:49-53
  - **innoxia** 28:113-123
  - **involuta** 28:113-123
  - **ozarkensis** 28:113-123
- **Lineatriton** (Plethodontidae) 10:37-44
- Linn County, Oregon, *Sylvilagus floridanus* 41:167-175
- Linnaeus, Carl 19:27-35
- *Liparthrum*
  - **arizonicum** 19:57-62
  - **artocarpus** 48:188-195
  - **mexicanum** 43:647-659
  - **pruni** 43:647-659
  - **thevetiae** 41:121-128
  - **tinianesis** 48:188-195
- *Lipsothrix* **hynesiana** 24:19-25
- Litter decomposition by arthropods
  - Mountain brush habitats 49:562-569
- Little Box Elder Cave, Wyoming
  - Late Pleistocene mammals 31:93-105
  - Mammal zoogeography 31:93-105
- Livestock, *Kochia americana* abundance 44:635-646
- Lizards
  - *Ctenosaura*, systematics, keys, Mexico 32:104-111
  - Environmental response
    - Saratoga Springs, California 30:146-165
  - Horned, notes on birth and growth 3:60
  - Leopard, systematics, Great Basin 37:225-240
  - Sagebrush
    - Aberrant karyotypes 46:224-227
    - Activity patterns, Southeastern Idaho 45:607-614
  - Sand, ecology 47:175-185
  - Sceloporine, evolution and phylogeny 35:1-20
  - *Sceloporus*
    - Systematics 34:97-104
    - Systematics, Mexico 34:231-237
  - Short-horned
    - Activity patterns, Southeastern Idaho 45:607-614
  - Species-habitat relationships
    - Oregon cold desert 42:380-384
  - Sympatric, reproduction, West Central Utah 40:68-72
  - Systematics, Western Chihuahua, Mexico 47:383-421
  - Western collared, observation of voice 34:276
  - Western whiptail, food habits
    - New Mexico 45:527-534
- Loasaceae
  - *Mentzelia*
    - Systematics, Book Cliffs, Utah 46:555-556
    - Systematics, Colorado Plateau 46:549-554
    - Systematics, Utah 46:361-365; 46:557-558
- Lobsters
  - American
    - Growth, semiopen and closed culture systems 42:67-72
  - Culture, Great Salt Lake water 39:231-240
- Locoweed, white
  - Soil-site relationships, Raft River Mountains, Utah 49:419-424
- *Lodia* **parapectinata** 48:232-249
- Logan Canyon, Utah
  - Cliff chipmunk, food preferences 31:182-188
- *Loganiella* **johnsoni** 37:475-480
- *Loganius*
  - **confinis** 21:87-107
  - **exilis** 27:119-141
  - **fastigius** 21:87-107
  - **impressus** 21:87-107
  - **liratus** 21:87-107
  - **niger** 21:87-107
  - **prociduus** 21:87-107
  - **splendens** 21:87-107
  - **vagabundus** 21:87-107
- Logging, soil compaction
  - Northeastern California 48:117-120
- *Lomatium scabrum* **tripinnatus** 46:66-106
- *Lophothetes* **reimschiiseli** 20:23-28
- *Lopidea nigridia* complex, systematics 50:135-154
- *Lordotus*
  - **abdominalis** 19:9-26
  - **arizonensis** 19:9-26
  - **arnaudi** 19:9-26

  cingulatus 19:9-26
  cingulatus ***lineatus*** 19:9-26
  cingulatus ***rufotibialis*** 19:9-26
  lutescens 19:9-26
  miscellus ***melanosus*** 19:9-26
  perplexus 19:9-26
  s射rorculus ***nigriventris*** 19:9-26
Louisiana, Plecoptera, systematics, keys 36:366-384
Lupinus argenteus ***moabensis*** 46:261-264
Lycosa, bite of 38:478
Lygodesmia ***entrada*** 40:78-88
Lymantor ***alaskanus*** 38:397-405

M

Macchiati, Luigi, aphid descriptions 12:55-57
Macrobiota, aquatic, Timpie Springs, Utah 42:77-80
Macroinvertebrates
  Colonization
    Rocky Mountain streams, Utah 45:117-123
  Longitudinal community development
    Below oligotrophic lake outlets 50:303-311
  Provo River, Utah, checklist 32:211-219
  Stream, effects of livestock grazing
    New Mexico 48:146-153
Macropharsa ***hackeri*** 13:91-99
Macrosiphum ***timpanogos*** 3:5-8
Macrotus waterhousii, distribution
  Southern Nevada 30:53
Maggots
  Apple, adaptation for cherries 46:173-174
  Onion, Provo, Utah 20:48
Magnadigita ***marmorea*** 21:23-26
Magpies
  Black-billed, distribution and abundance
    North America 35:269-272; 36:111
  Predation on small mammals 45:152-153
Malacosoma californicum
  Length of egg masses 41:465-466
Malheur County, Oregon, herpetological notes 9:59-63
Malheur National Wildlife Refuge, Oregon
  Franklin's Gulls 41:440-444
Mallophora ***pallida*** 18:41-42
Mallow, common, cold acclimation 40:121-126
Malvaceae, systematics, keys, Utah 40:27-37
Mammals
  Bibliography, checklist, Utah 2:125-136
  Collection, John E. Blazzard 1:146
  Crystal Ball Cave, Utah
    Quaternary paleontology and paleoecology 45:337-390
  Distribution, Nevada Test Site 50:83-84
  Distributional patterns, Utah 37:457-474
  Feces containing nitrogen-fixing bacteria 46:646-650
  Fossil, Quaternary mustelids, Great Basin 49:143-154
  Humerus from Upper Jurassic, Colorado 43:551-553
  Insular biogeography
    Great Salt Lake, Utah 42:589-596
  Late Pleistocene and recent, zoogeography 31:93-105
  Nuevo Leon, Mexico, annotated list 2:9-15
  Paunsagunt Plateau Region, Utah 26:43-44
  Plague important, Western United States 12:67-75
  Preliminary survey
    Fossil Butte National Monument, Wyoming 37:91-94
  Small
    Abundance and distribution, Southeastern Oregon 39:207-218
    Burrow diameter of five species, Idaho 49:646-649
    Food habits, Piceance Basin, Colorado 44:145-150
    Fungi in, from *Nothofagus* forest, Argentina 49:618-620
    National Reactor Testing Station, Idaho 33:246-250
    Radioactive waste dispersion, Idaho 46:404-410
    Ruby Lake, Nevada 49:123-130
  Systematics, Utah 2:105-108
  Traps, disturbance by jackrabbits 22:83-86
  Type specimens
    Utah Museum of Natural History 47:620-624
Manti-La Sal National Forest
  Raptor species survey 39:155-160
Maple, bigtooth, root system 22:114-115
Marmot scats, food energy source for pikas 49:466-468
Marsh plants, Utah
  Comparison of burning and cutting 45:462-466
Marshall, Guy, Sir 20:78
Martens
  American, demographics
    Jackson Hole, Wyoming 49:587-596
  Food caching and handling 50:381-383
  Pine
    Feeding habits 46:166-168
    Fleas associated with plague 44:170-175
Martes americana
  Feeding habits, winter 46:166-168
  Food caching and handling 50:381-383
Mason Fen, California, peat depth 36:101-107
Mastigodryas 33:276
Mayflies, growth and population densities
  Variable temperatures 50:97-106
McKnight Creek, New Mexico
  Stream channel and vegetation changes 48:373-381
Meadowlark, Western, insect food, Utah 4:101-102
Mecistocephalus
  kraussi 13:75-85
  malayensis 13:75-85
  waikaneus 13:75-85
Mecopharsa (Tingidae) 13:91-99
Medeterus ***arnaudi*** 11:11-17
Medicago sativa
  Nodulation, acetylene reduction, Great Basin 44:151-158
Megabothris
  Distribution in the Bonneville Basin, Utah 37:75-76
Megarcys signata, life history and ecology 35:39-48
Megarthroglossus

- ***becki*** 11:105-114
- Systematics 39:351-418

Megeremaeus ***ditrichosus*** 28:172-175

Melanoplus, distribution, economics, Utah 5:1-22

Meleagris gallopavo merriami
- Habitat and home range, Oregon 49:252-258

Mentzelia
- ***cronquistii*** 46:549-554
- *multicaulis* ***librina*** 46:555-556
- *pumila* ***lagarosa*** 46:557-558
- ***shultziorum*** 46:361-365

Meringis
- ***disparalis*** 38:447-455
- ***facilis*** 38:447-455

Mesa Verde National Park, Colorado, fleas 26:76-78

Mesembrioxylon ***stokesi*** 44:231-256

Mesobius danianus 11:115-118

Mesquite
- Casa Grande National Monument, Arizona 31:153-159

Metapyroppia ***doratosa*** 29:137-139

Meteorologic measurements, computer reduction
- Plots in Central Utah 35:203-230

Mexico
- Baja California
  - Cape wormsnake, correct name 34:94-96
  - Snakes, systematics and distribution 38:406-410
- Baja California Sur, *Xerobates* 49:496-502
- Jalisco
  - *Sceloporus horridus*, feeding habits 36:108-110
- Nuevo Leon, mammals, annotated list 2:9-15
- Sonora, colubrid snakes 26:136-140
- Urique, Chihuahua, amphibians and reptiles 19:75-82
- Western Chihuahua
  - Amphibians, systematics 49:38-70
  - Snakes 45:615-676
- Western Tabasco
  - *Rhinoclemmys areolata* courtship behavior 48:263-266

Mice
- Deer
  - Altitudinal hemoglobin variation 39:192-194
  - Ecology and taxonomy, Idaho 38:469-472
  - Flea exchange with rodents, Western Utah 36:475-480
  - Fleas, Colorado 43:168-174
  - Genetic variation, Great Basin 46:577-580
  - Prairie dog rodenticide effects on, Western South Dakota 50:347-353
  - Short-term effects of logging on 40:183-189
- Grasshopper
  - Epizoology of wild rodent plague 48:83-95
- Great Basin pocket, distribution, Utah 18:26-30
- Pinyon
  - North Central Nevada, distribution 44:428-430
- Pocket
  - Reproduction, Bonneville Basin, Utah 50:361-365
- Southern grasshopper
  - Water balance and fluid consumption 35:62-64
- Western harvest
  - Growth and development 34:105-120
- Western jumping, home range, Colorado 37:87-90

Micracis
- ***burgosi*** 42:223-231
- ***carinulatus*** 20:59-69

Microborus
- ***lautus*** 21:87-107
- ***mexicanus*** 41:121-128

Microcorthylus
- ***concisus*** 33:265-275
- ***contractus*** 33:265-275
- ***curtus*** 33:265-275
- ***debilis*** 33:265-275
- ***demissus*** 33:265-275
- ***desus*** 27:36-57
- ***dilutus*** 33:265-275
- ***diversus*** 33:265-275
- ***hostilis*** 33:265-275
- ***inermis*** 33:265-275
- ***invalidus*** 33:265-275
- ***lassus*** 33:265-275
- ***ocularis*** 33:265-275
- ***pumilus*** 33:265-275
- ***pusillus*** 33:265-275
- ***umbratus*** 33:265-275
- ***vescus*** 33:265-275
- ***vicinus*** 37:207-220

Microdipodops
- *megacephalus*
  - Dominance relationships with *Perognathus longimembris* 34:312-316
- *megacephalus nasutus*, distribution 41:333-334

Microorganisms, distribution in desert soil 37:81-86

Microperus (Scolytidae) 40:89-97

Microrhopala ***rileyi*** 43:597-618

Microtus
- *montanus*
  - Hip glands 44:468-470
  - Indomethacin wheat, population control 49:556-561
- *montanus* ***amosus*** 2:105-108
- *montanus* ***nexus*** 2:105-108
- *pennsylvanicus*
  - Prevalence of *Taenia taeniaeformis* in, Montana 37:252

Microvelia
- ***ayacuchana*** 12:47-54
- ***cubana*** 11:37-42
- ***depressus*** 34:207-217
- ***duidana*** 12:47-54
- ***glabrosulcata*** 34:207-217
- ***leavipleura*** 34:207-217
- ***oaxacana*** 11:37-42
- ***paura*** 34:207-217
- ***portoricensis*** 11:37-42
- ***psilonota*** 34:207-217
- ***reflexus*** 34:207-217

  tateiana 11:37-42
Microzetes auxiliaris appalachicola
  Redescription 28:142-143
Midges, gall
  Bionomics, from *Artemisia ludoviciana* 37:429-442
Milkvetch, Wahweap
  Population cycles, seed reserves
    Henry Mountains, Utah 48:541-547
Mill Creek, Wasatch Mountains, Utah
  Megarcys signata, life history and ecology 35:39-48
Miller, Lowell Storrs 15:50-54
Millipeds
  Systematics
    America 12:13-34
    Southern United States 11:19-26
    United States 11:27-35
Miloderes
  allredi 34:291-296
  tingi 34:291-296
Miloderoides ***vandykei*** 3:23-26
Mima mounds
  Iowa, vegetation 42:246-261
  Oregon 47:609-619
  Relation to slope steepness and aspect
    Oregon 50:21-32
Mimiocurus ***beesoni*** 49:167-185
Mimulus
  cardinalis-M. lewisii complex
    Pollination experiments 50:155-159
  Esterase variation 36:81-85
  guttatus
    Evolutionary divergence 35:240-244
    Seed germination 43:470-474
Mine highwall, wildlife response
  South Central Wyoming 49:449-455
Mink, internal parasites, checklist
  Southwestern Montana 33:53-60
Mistletoe
  Douglas-fir dwarf
    Parasitizing Pacific silver fir, Northern California 47:161-162
  Dwarf
    Douglas-fir infection, Southwestern United States 50:67-71
    Effects on Douglas-fir, Southwestern United States 50:173-179
    Effects on spruce, White Mountains, Arizona 46:685-689
    Forest smoke, effects on seed germination 47:652-659
    Infecting Douglas-fir, spruces, Southwestern United States 46:528-534
    Pandora moth interaction, ponderosa pine mortality, Arizona 45:432-426
  Juniper
    Hosts, Walnut Canyon National Monument, Arizona 38:89
  Limber pine dwarf, distribution, Nevada 50:91-92
  White fir dwarf
    Range extension in Arizona 36:461-462
Mites
  Control by *Typhlodromus mcgregori* 37:366-374
  Dugway, Utah 13:35-42
  Oregon, checklist from mammals 45:67-76
  Parasitizing *Peromyscus*, Utah 16:23-31; 17:95-102
  Phytoseiid
    Overwintering in Central Utah apple orchards 29:96-104
    Predators in Utah orchards 39:63-80
  Systematics, United States 25:55-58
  Utah, unusual records 26:34
Mocoa smithii 31:135-137
Moffat County, Colorado
  Presettlement vegetation 45:747-777
Mogollon Plateau, Arizona
  Biomass in montane forests 44:627-634
Mohave Desert, California
  Coniferous woodlands
    Pleistocene-Holocene 36:227-238
  Effects of land clearing on winter annuals 47:234-238
Moisture gradient
  Vegetation response, Central Arizona 39:161-176
Mojave Desert
  Bird behavior related to temperature 42:232-240
Mojave Desert, Nevada
  Ambrosia dumosa, intraspecies competition 49:79-84
Mollusca
  Biogeography, Intermountain Region 46:736-744
  Fish Springs, Utah 31:223-236
  Recent, Wyoming, checklist 49:637-645
Molophilus
  aspersulus 22:1-7
  frohnei 28:16-23
  nitidulus 5:93-103
  subnitens 5:93-103
Moluccobius ***marshalli*** 20:23-28
Monarthrum
  adustum 34:135-150
  bicavum 27:36-57
  bicolor 28:1-15
  bidentatum 34:135-150
  bifoveatum 34:135-150
  carinatum 34:135-150
  carinulum 34:135-150
  conversum 34:135-150
  corculum 34:135-150
  cordicticum 34:135-150
  fastigiorum 34:135-150
  huachucae 19:57-62
  infradentatum 34:135-150
  insignatum 34:135-150
  limulum 34:135-150
  morsum 34:135-150
  notatum 34:135-150
  posticum 34:135-150
  preclarus 28:1-15

  proprium 34:135-150
  proximum 34:135-150
  quercicolens 27:36-57
  querneus 27:36-57
  subgranulatum 34:135-150
  tetradontium 34:135-150
  xalapensis 47:547-550
Mono Lake, California, salt grass invasion 45:542-545
Monosteira ***edeia*** 24:27-30
Monoterpene concentrations
  Western Great Basin pinyon litter and soils 48:228-231
Montana
  Anopheles, records and observations 7:23-28
  Bibliography of vegetation description 48:301-323
  Black-tailed prairie dogs
    Reproductive ecology 47:202-206
  Brown trout, reproduction 35:435-441
  Flathead chub biology 45:332-336
  Glacier National Park
    Unusual tooth wear in elk 41:368-369
    Vegetational and geomorphic change, avalanche paths 45:313-317
  Kingbirds, frequency distribution 3:109-114
  Pine Butte Fen, vegetation and flora 46:22-32
  Scolytidae, checklist 49:381-386
  Yellowstone River
    Parasites of *Polyodon spathula* 35:425-426
Montana, Southeastern
  Plant community variability 43:660-668
Montana, Western
  Boreal toad, breeding behavior 31:109-113
Montezuma Well, Arizona, aquatic insects 49:85-88
Morels, false, Utah 31:35-47
Mormon crickets
  Migrating, food for stream fishes 48:25-30
Morone chrysops
  Diel behavior, Utah Lake, Utah 44:509-515
Mosquitoes
  Dipterous predators, Utah and Wyoming 9:21-23
Mosses
  Grand Teton National Park and vicinity, Wyoming
    Checklist 45:124-126
  Intermountain West, checklist 48:394-401
Moths
  Pandora
    Dwarf mistletoe interaction, ponderosa pine mortality, Arizona 45:432-426
    Emergence in Arizona 44:161-165
  White-lined sphinx
    Abundant in spring, 1940, Central Utah 9:76
Mount Dellenbaugh, Arizona
  Avifauna of the region 41:259-268
Mount Timpanogos, Utah
  Ambystoma tigrinum nebulosum, life history 31:213-222
  Aphids, checklist 7:1-6
Multoribates ***haydeni*** 35:103-108
Mustela erminea, Western Utah 28:47
Mutualism
  Mammal-mycorrhizal fungus-tree, nitrogen fixation 46:411-414
Mycophagy
  Clethrionomys 48:269-273
  Peromyscus 47:308-313
Mycorrhizal fungi
  Interactions with squirrels
    Oregon coniferous forests 48:358-369
  Vesicular-arbuscular
    Atriplex canescens inoculation 44:363-371
Myriapods, Nevada Test Site, ecology 31:161-163
Myrmecocystus ***pyramicus*** 11:91-96
Myzus ***haywardi*** 3:5-8
Nannolene ***corticolens*** 11:27-35
Naochila
  arete 21:108-113
  engys 24:83-92
National Engineering Laboratory, Idaho
  Coleoptera, checklist 46:287-293
  Rare vascular plants 44:140-144
  Reptile responses to land management 39:255-262
National Reactor Testing Station, Idaho
  Ants 31:237-242
  Ectoparasites 31:77-82
  Fleas 28:73-87
  Scorpions 33:251-254
  Small mammals 33:246-250
  Solpugids 31:164-168
  Spiders 29:105-108
Natural history, Great Basin, 1800-1855 1:33-61
Navajo National Monument, Arizona
  Bird community composition
    Betatakin Canyon 41:298-309
  Cryptogamic soil crusts 43:73-78
  Plant communities 45:1-13
  Subaerial algae 41:433-439
  Vascular plants, checklist 38:19-30
Nebraska
  Chadron, *Cercocarpus montanus* 37:97-99
  Prairie skinks, reproduction 47:373-374
  Scotts Bluff National Monument
    Terrestrial vertebrates, checklist 49:597-613
Nebraska, Northwestern
  Pinus ponderosa, distributional aspects 28:24-29
Nectar-sugar concentrations
  Flower visitors, Western Great Basin 37:523-529
Nematodes
  Chandlerella, systematics, keys 36:445-457
  Predacious, systematics 10:45-50
  Soil, Northern Rocky Mountain ecosystems
    Genera and biomass 47:473-479
  Splendidofilaria, systematics, keys 36:445-457
  Tylenchidae, systematics 2:37-85
Neoperla
  carlsoni 38:97-114
  catharae 38:97-114

  choctaw 38:97-114
  freytagi 38:97-114
  gaufini 38:97-114
  stewarti 38:97-114
Mountain brush vegetation
  Comparative study, Utah 27:59-66

N

Neoteneriffiola ***uta*** 18:43-45
Neotoma
  cinerea
    Genetic variation, Great Basin 46:577-580
  lepida lepida
    Siphonaptera associated with nests 15:35-49
Neotrachyostus ***obliquus*** 26:45-70
Neotropical Region
  Hydrometridae, checklist 19:43-52
Neotylenchus
  acutus 2:37-85
  arcuatus 2:37-85
Nesocypselas
  evansi 13:91-99
  evansi ***aemulus*** 13:91-99
Nesomerium hawaiiense 13:75-85
Neurigona ***torrida*** 11:11-17
Nevada
  Aculeata Hymenoptera, checklist 43:403-408
  Alvord Basin, life history of native fishes 43:409-420
  Ash Meadows
    Amargosa pupfish, systematics 46:220-223
  Big Soda Lake
    Primary productivity 38:187-192
    Zooplankton orientation to the oxycline 49:535-539
  Birds, distribution 14:15-18
  Carson Range
    Great Basin black bear den co-occupancy 49:390-391
  Cerambycoid semi-aquatic Coleoptera 11:97-104
  Chimney Creek, Lahontan cutthroat trout
    Spawning behavior 47:480-487
  Clark County, Verdin, body composition 31:66-68
  Clark's Grebe, breeding records 46:581-582
  Devil's Hole
    Cyprinodon diabolis movement 43:592-596
  Fish hatchery history 46:583-594
  Formica propinqua nests 41:389-392
  Great-tailed Grackle 45:483-484
  Histeridae, checklist 7:7-10
  Hot Creek Spring, White River springfish
    Foods and feeding 49:249-251
  Kawich Mountains
    Birds of the pinyon association 16:32-33
  Lake Gilbert, plant communities, landforms 46:1-21
  Lake Mead and Lake Mohave
    Largemouth bass food habits 48:485-488
  Limber pine dwarf mistletoe, distribution 50:91-92
  Mojave Desert, *Ambrosia dumosa*
    Intraspecies competition 49:79-84
  Mountain ants, checklist and ecology 38:379-396
  Ornithology, bibliography 28:49-60
  Pahranagat Valley
    Cattle impact on fish populations 49:491-495
  Perognathus longimembris
    Habitat invasion 29:143-149
  Pinyon-juniper woodland densities 46:178-184
  Plecoptera, checklist 35:49-50
  Pyramid Lake
    Cui-ui, life history 45:571-603
    Fish species composition and abundance 41:395-408
    Food of larval tui chubs 43:175-178
    Gila bicolor seasonal growth 43:713-716
    Reproductive biology of *Gila bicolor* 38:203-207
    Reproductive ecology of *Catostomus tahoensis* 38:181-186
    Sacramento perch life history 41:278-289
    Salmo clarki henshawi, life history 43:1-29
    Vertical distribution of adult fish 38:417-428
  Ruby Lake, small mammals 49:123-130
  Selenium in soils, plants and animals 49:201-213
  Soda Lake, limnology 31:106-108
  Test Site
    Arthropod sampling problems 27:26-35
    Beeflies 25:5-11
    Bees 29:20-24
    Birds, wintering habits 22:30-31
    Brachycistidine wasps, checklist 33:109-112
    Coleoptera 29:11-19
    Coleoptera, checklist 34:218-220
    Ecological research, references 26:79-86
    Faunistic inventory 28:132-141
    Insects 26:9-16
    Isopods 25:43-47
    Kangaroo rat burrows 24:93-101
    Lepidoptera 29:42
    Mammals, distribution 50:83-84
    Mites from mammals 24:71-73
    Mites on grasshopper mice 22:101-104
    Mutillid wasps 33:156-162
    Myriapods, ecology 31:161-163
    Phalangida, ecology 25:37-38
    Reptiles 29:31-34; 42:219-222
    Sceloporus magister, ecology 33:133-146
    Spiders 27:11-25
  Understory vegetation in pinyon-juniper 41:467-475
  Upper Walker River
    Vascular flora, checklist 43:93-130
  Vegetation, bibliography 50:209-242
  Walker Lake
    Gila bicolor, reproduction and embryology 42:60-64
    Tui chub biology 45:784-788
  White-tailed deer, probable record 28:199
Nevada, Central
  Birds of a shadscale habitat 50:295-298

  Individual rodent movements 29:109-110
  Seasonal variation in desert arthropods 40:292-297
Nevada, East Central
  Breeding birds, bristlecone pine stand 44:272-276
Nevada, Eastern
  Bristlecone pine ecology 44:487-494
Nevada, North Central
  Ammospermophilus leucurus, distribution 44:428-430
  Peromyscus truei, distribution 44:428-430
Nevada, Northeastern
  Mountainous sagebrush community characteristics 48:403-421
  Plant associations, big sagebrush-longleaf snowberry 47:117-131
  Sagebrush community type classification 48:422-433
  Soil characteristics, sagebrush communities 49:469-481
Nevada, Northern
  Artemisia habitat types 33:225-242
Nevada, South Central
  Microbiology, water chemistry of two natural springs, grazing impacts 50:289-294
Nevada, Southeastern
  Soil frost and infiltration rate, dune and interspace soils 50:41-46
Nevada, Southern
  Birds, uncommon records 26:41-42
  Macrotus waterhousii, distribution 30:53
  Status of introduced fishes 42:361-366
New Mexico
  Chaco Canyon, spatial and temporal variability of vegetation 49:113-122
  Chihuahuan Desert
    Tiger salamander, life history 31:193-212
  Dona Ana County
    Uta stansburiana stejnegeri 33:124-128
  Grass taxonomy and types
    Selected bibliography 50:73-82
  Las Vegas
    Amphibians, observations 2:109-117
    Reptiles 9:55-57
  Lava Tube Caves
    Invertebrates and zoogeographic significance 42:405-412
  Livestock grazing
    Macroinvertebrates in montane stream 48:146-153
  McKnight Creek
    Stream channel and vegetation changes 48:373-381
  Plant survival on coal mine spoils 41:271-273
  Plecoptera, checklist 35:97-99
  San Juan County, birds 37:489-500
  Soil fungi between and beneath pinyon-juniper canopies 50:167-172
  Winter stoneflies, distribution 43:585-591
New Mexico, Southeastern
  Cnemidophorus tigris, food habits 45:527-534
New Mexico, Southwestern
  Rodent weights in modified pinyon-juniper woodlands 48:554-557
New records
  Acarina
    Idaho 36:57-64
    Utah 36:57-64
  Agathoxylon, North America 46:559-566
  Algae, Utah Lake, Utah 30:99-105; 45:237-254
  Ambystoma tigrinum, Idaho 44:313-316
  Amphibians
    Baker County, Oregon 18:63-65
    Chihuahua, Mexico 19:75-82
    Southern Mexico 17:52-56
  Anomiopsyllus amphibolus, Southeastern Oregon 40:361
  Anopheles, Montana 7:23-28
  Antrozous pallidus, Montana 40:115
  Ants, Utah 27:67-78
  Arceuthobium, Arizona and New Mexico 43:741-476
  Arceuthobium abietinum, Arizona 36:461-462
  Astragalus lentiginosus fremontii, Utah 34:180
  Astragalus lentiginosus vitreus, Utah 34:180
  Atherinidae, Mexico and Texas 25:73-76
  Aves, Zion National Park, Utah 2:121-122
  Basidomycetes, Arizona 38:42-48
  Basilia dunni, Venezuela 37:221-224
  Bats, Northwestern Colorado 43:554-560
  Bipalium kewense, Utah 12:62
  Birds
    Clark County, Nevada 26:41-42; 28:61-62
    Great Salt Lake, Utah 37:247-251
    Nevada 14:15-18
    Uinta Basin, Utah 18:23-25
    Utah 33:243-245
    Utah and Idaho 43:717-727
  Blue-gray Gnatcatcher, Wyoming 43:747-748
  Brachylagus idahoensis, Southwestern Wyoming 42:100
  Carabidae, Colorado 47:631-637
  Chordeiles, Utah 1:93-96
  Chrysemys picta belli, Grant County, Oregon 47:344
  Cichlasoma managuense, North America 49:387-389
  Cicuta bulbifera, Alaska 48:382
  Climacia californica, Idaho 45:391-394
  Coenia, North America 35:65-85
  Coleoptera, Utah 2:36
  Collembola, Utah 13:43-46
  Coniana snowi, Utah 18:66-67
  Coreidae, Nevada Test Site 33:123
  Crataegus colorado, Utah 4:55
  Crotalus atrox
    Nevada, correction 42:350
    Southern Nevada 30:107
  Culicidae, Colorado 9:65-75
  Dermacentor hunteri, United States 23:166
  Diadophis regalis regalis, Nevada 12:63-64
  Diatomaceae
    Blue Lake Warm Spring, Utah 44:120-124
    Great Basin 46:398-403
    North America 44:120-124

Diplocardia verrucosa, New Mexico 27:1-10
Earthworms, United States 27:142-176
Elymus flavescens, Utah 43:619-646
Ephydatia mulleri, Idaho 45:391-394
Epilachna corrupta, Utah 1:91
Eridiphas slevini
  Baja California, Mexico 38:406-410
Euderma maculatum
  California 48:563
  Colorado 42:360
  Oregon 41:270
Fish, Idaho and Wyoming 47:523-526
Fleas, Utah 26:71-75
Forficula auricularia, Utah 5:22
Gastropods, Deep Creek Mountains, Utah 14:19
Gavia immer immer, Southern Colorado 13:74
Glaucomys sabrinus lucifugus, Garfield County, Utah 1:126
Gordiacea, Utah 1:2
Grasses
  Arizona, New Mexico, Texas 40:221-222
  New Mexico 37:530-531
  United States 37:530-531
Grimmia atricha, Nevada 42:583-588
Hebrus, Americas 13:9-11
Helianthus deserticola, Arizona and Utah 41:393-394
Helianthus niveus canescens, Arizona and Utah 41:393-394
Helix aspersa, Utah 14:90
Heteromyidae, Great Basin 48:267-268
Heterosphyronida, New Mexico 12:39-45
Hindia sphaeroidalis, Nevada 36:206-210
Hudsonian Godwit, Nevada 37:532
Hydrometra martini, Central Utah 18:67
Hypsiglena torquata, Idaho 44:313-316
Indigo Bunting, Northern Utah 32:220
Ixodes muris, Utah 12:65-66
Larus, Utah 48:298-300
Leptophlebiidae, North America 47:283-286
Leptotyphlops humilis, Death Valley, California 30:91-93
Mammals
  Antelope Island, Great Salt Lake 46:307-309
  Nevada Test Site 50:83-84
  Utah 50:283-285
Megabothris clantoni princei, Western Utah 37:75-76
Melanoplus, Utah 5:1-22
Microdipodops megacephalus, Wassuk Mountains, Nevada 41:333-334
Millepeds, America 12:13-34
Mites
  Dugway, Utah 13:35-42
  Oregon 45:67-76
Monotropa hypopithys, Colorado 46:175-177
Montia linearis, Utah 41:269
Muscivora forticata, Death Valley, California 23:165
Mustela nigripes, Wyoming 41:360-361
Mutillid wasps, Nevada Test Site 33:156-162
Neotoma cinerea, White Mountains, California 49:392-395
Notiosorex crawfordi, Rincon Mountains, Arizona 49:140-141
Odonata, Colorado 48:96-101
Onychomys torridus longicaudus, Northwestern Nevada 38:180
Paracoenia, North America 35:65-85
Patapius spinosus, Idaho and Nevada 39:195-196
Perognathus parvus, Utah 18:26-30
Phaedactylum tricornutum, Utah 48:324-326
Pinus longaeva, Stansbury Mountains, Utah 38:49-50
Pityophthorus, Mexico 45:476-482
Pityophthorus corruptus, Mexico 46:641-645
Plain Titmouse, Wyoming 43:747-748
Plants, Utah 30:16-22; 32:117-119
Platypodidae, Neotropical Region 26:45-70
Platypus, North America 18:37-40
Plecoptera
  Louisiana 36:366-384
  Nevada 35:49-50
  New Mexico 35:97-99
Plecotus phyllotis, Utah 35:452
Pompilidae, Rocky Mountain States 50:193-195
Procyon lotor, Wyoming 42:599-600
Pseudocrossidum aureum, Wayne County, Utah 47:347-348
Pseudopityophthorus, Mexico 19:1-7
Ranatra quadridentata, Utah 7:29
Reptiles
  Baker County, Oregon 18:63-65
  Chihuahua, Mexico 19:75-82
  Death Valley, California 23:119-128
  Jalisco, Mexico 35:317-318
  Mexico 31:138-139
  Nevada Test Site 29:31-34; 42:219-222
  Southern Mexico 17:52-56
  Western Chihuahua, Mexico 47:383-421
Rhacomitrium heterostichum, Nevada 42:583-588
Rhinocheilus lecontei lecontei
  East Central Utah 34:238-240
  Owyhee County, Idaho 36:56
Salientia, Oklahoma 11:87-90
Salvia sclarea, Utah 6:128
Say's Phoebe, Northern Utah 32:220
Scolytidae
  Arizona 19:57-62
  Chihuahua, Mexico 20:59-69
  Idaho 47:375-382
  Montana 49:381-386
  Neotropical Region 28:1-15
  Western North America 20:59-69
Scorpions, Utah 32:154-170
Siphonaptera
  Utah 10:62-65; 11:105-114
  Western United States 45:530-532
Snakes
  Southwestern Idaho 41:154-157

    Utah 2:16-28
  Solpugids, Nevada 32:120
  Sorex, Great Basin 48:267-268
  Sorex nanus, Fracas Lake, Arizona 50:161-165
  Spongilla fragilis, Utah 1:61
  Stilt Sandpiper, Nevada 37:532
  Stoneflies, New Mexico 43:585-591
  Tingidae, Nevada 31:160
  Tipulidae, Middle America 30:232-241
  Totanus flavipes, Washington County, Utah 2:86
  Trichoptera
    Southeastern Idaho 37:253-257
    Western United States 40:287-291
  Trimerotropis arenacea, Utah 22:108-109
  Trionyx spiniferus emoryi, Utah 37:259
  Trombiculidae, Utah 15:1-26
  Vararia fibra, United States 38:42-48
  Vascular flora
    Montana 42:413-414
    Teton County, Wyoming 40:408-413
    Wyoming 42:413-414; 44:482-483
    Wyoming and Montana 43:739-740
  Vascular plants
    Alberta, Canada 36:243-271
    Colorado 38:208-210; 44:516-517
  Veliidae, Arizona 47:660
  Vertebrates
    Idaho 2:87-97
    Western United States 1:138-146
  Weevils, United States 14:73-78
  White-tailed deer, Nevada 28:199
  Wislouchiella planctonica, Nevada 29:43
  Wolverine, LaSal Mountains, Utah 18:56
Newby, William Wallace 45:443-454
Newportia
  albana 17:30-41
  atopa 17:30-41
  caldes 17:30-41
  ecuadorana 17:30-41
  rossi 17:30-41
  schlingeri 17:30-41
Niche pattern
  Desert rodent fauna, Great Basin 47:488-496
Nightshade, bitter
  Naturalization, habitat, Central Utah 44:317-323
Nitrification in soils
  Acetylene inhibition 46:316-320
Nitrogen availability
  Artemisia tridentata wyomingensis, effects on growth and photosynthesis 50:9-20
Nitrogen fixation
  Mammal-mycorrhizal fungus-tree mutualism, Oregon 46:411-414
  Medicago and *Hedysarum*, Great Basin 44:151-158
  Symbiotic, desert plants 36:65-80
Nitrogen-fixing bacteria, mammal feces 46:646-650
North America
  Black-billed Magpies
    Distribution and abundance 35:269-272; 36:111
  Cinara occurring on *Picea*, keys 21:35-50
  Stoneflies
    Checklist, distribution, bibliography 46:383-397
Nothofagus forest, Argentina
  Fungi in small mammals 49:618-620
Nothotylenchus (Nematoda) 2:37-85
  acris 2:37-85
  affinis 2:37-85
  cylindricollis 2:37-85
Notolepidomyzon ***intermedius*** 3:27-32
Numenius americanus, nesting biology 32:88-90
Nutrient cycling
  Arthropod effects
    Mountain brush habitats 49:134-139
Nymphalis antiopa
  Phenology and migration, California 46:112-116

O

Oak, Gambel
  Recovery after fire 40:127-130
  Seedling microhabitat affinities 46:294-298
Oakbrush, compositional similarity, Utah 41:147-153
Obsidian, Idaho
  Diplostomum spathaceum in fishes 43:675-683
Ochotona
  princeps
    Marmot scats as winter food supplement 49:466-468
  princeps saxatilis
    Blood protein, interpopulational variation 37:77-80
  princeps ***utahensis*** 2:105-108
Ochterus ***rotundus*** 36:221-226
Odocoileus
  hemionus
    Bottle feeding of fawns 46:217-219
    Differential habitat utilization by sexes 40:273-281
    Fecal pellet similarities to pronghorn 38:222-224
    Fetal growth rates 46:245-248
    Utah, changes in size 49:31-35
  hemionus hemionus
    Bed characteristics 46:542-546
    Captive behavior 47:105-109
Odonata, Colorado, checklist 48:96-101
Oeciacus vicarius
  Barn and Cliff Swallow nest occupants, Colorado 47:345-346
Oenothera, nectar composition
  Hawkmoth-visited species 35:273-274
Oestranthrax ***farinosus*** 13:17-27
Oil Shale Tracts, Utah
  Wildlife distribution and abundance 46:469-507
Oiovelia cunucunumana 12:47-54
Oklahoma
  Anuran ecology and natural history 3:33-50; 4:62-80
  Caudata, distribution 11:87-90
  Flint Creek
    Nongame insectivorous fish,

    food habits 45:721-733
  Greer County, amphibians 15:27-31
Olonthogaster
  jiri 48:196-201
  regalis 48:196-201
Onblavia ***freytagi*** 49:398-403
Onchocerca cervipedis
  Parasitizing mule deer, Central Utah 42:351-352
Oncorhynchus tshawytscha, juvenile
  Effects of artificial shading 47:22-31
Onychiurus
  irregularis 4:39-48
  millsi 4:39-48
Onychomys
  leucogaster
    Epizoology of wild rodent plague 48:83-95
  torridus
    Water balance and fluid consumption 35:62-64
Onychylis ***essigi*** 14:73-78
Ophidilaelaps
  farrieri 14:67-72
  tanneri 14:67-72
Ophidiotrichus ***exastus*** 25:55-58
Ophiotaenia
  critica 41:445-448
  Parasites, Colorado River squawfish 41:445-448
*Oppia****coloradensis*** 29:133-136
Opuntia basilaris ***heilii*** 43:700
Orange Cliffs, Utah, flora, checklist 47:287-298
Oreana local fauna (Blancan), Owyhee County, Idaho
  Fossil birds 46:763-768
Oregon
  Alvord Basin, life history of native fishes 43:409-420
  Baker County, herpetology 18:63-65
  Blue Grouse, fall feeding habits 46:123-127
  Cascade Range, *Felis concolor*, food 45:77-80
  Cold desert lizard communities
    Species-habitat relationships 42:380-384
  Curry County
    Aneides ferreus, food habits 46:228-240
  Ectoparasites of mammals 24:75-81
  Grant County, herpetology 30:9-12
  Harney County, Diamond Pond
    Vegetation history 47:427-458
  Linn County, *Sylvilagus floridanus* 41:167-175
  Malheur County, herpetological notes 9:59-63
  Malheur National Wildlife Refuge
    Franklin's Gulls 41:440-444
  Merriam's Wild Turkey
    Habitat and home range 49:252-258
  Mites from mammals, checklist 45:67-76
  Oregon Caves National Monument
    Diatoms, checklist 41:317-332
  Pygmy rabbit, habitat and distribution 44:563-571
  Squirrels and mycorrhizal fungi
    Coniferous forests 48:358-369
  Warner Basin
    Threatened fishes, conservation status 50:243-248
  Wasco County, mima mounds 47:609-619
Oregon, Eastern
  Beavers, dam site selection 50:273-281
  Bunchgrasses
    Effects of burning and clipping 50:115-120
Oregon, North Central
  Mima mounds, relation to slope steepness and aspect 50:21-32
Oregon, Northeastern
  Blue Grouse, hatching chronology 46:745-748
  Cougar winter food habits 43:425-428
Oregon, Southeastern
  Disjunct ponderosa pine stand 47:163-167
  Gila boraxobius feeding ecology 40:101-114
  Screech and Burrowing Owl food habits 46:421-426
  Small mammals, abundance, distribution 39:207-218
Oregon, Western
  Arboreal arthropods in coniferous forests 48:327-333
  Nitrogen fixation
    Mammal-mycorrhizae-tree mutualism 46:411-414
Oregon Caves National Monument, Oregon
  Diatoms, checklist 41:317-332
Oreoxis ***trotteri*** 45:34-36
Organ Pipe Cactus National Monument, Arizona
  Grass spider microhabitat 45:546-547
Oribatei, *Gymnodamaeus*, systematics, Utah 21:27-28
Oribatella ***anomola*** 30:5-8
Ormosia
  burneyana 24:19-25
  frohnearum 28:16-23
  hynesi 22:1-7
  nobilis 24:117-122
  pugetensis 5:93-103
Ornithology, Nevada, bibliography 28:49-60
Orthoporus
  bisulcatus 12:13-34
  bobos 12:13-34
  cienegonus 12:13-34
  crotonus 12:13-34
  euthus 12:13-34
  gracilior 12:13-34
  tehuacanus 12:13-34
  unciferens 12:13-34
Orthoptera
  Cibolacris, systematics, Chihuahua, Mexico 21:29-33
  Daihinibaenetes
    Systematics, Nearctic Region 22:12-29
  Decticidae
    Systematics, keys, Nearctic Region 33:197-201
  Eremopedes, systematics, keys 32:223-228
  Hesperotettix
    Systematics, corrections 6:126
    Systematics, Utah 3:9-21
  Melanoplus, systematics, Utah 5:1-22
  Petropedes, systematics, California 32:176-179
  Plagiostira
    Systematics, keys, Utah 22:105-107
    Systematics, New Mexico 20:39-47

  Platyoplus, systematics, Arizona 33:43-50
  Sand treader camel crickets
    Systematics, keys 30:242-249
  Stenopelmatinae
    Systematics, Kelso Dunes, California 25:63-71
    Systematics, keys, Nearctic Region 30:173-179
  Stenopelmatus
    Systematics, keys, United States 39:226-230
  Systematics, keys, Utah 14:39-60
  Systematics, Nearctic Region 28:124-131
  Trimerotropis
    Systematics, Idaho 24:31-35
    Systematics, New Mexico 21:51-54
    Systematics, Utah 20:49-58
  Viscainopelmatus, systematics, Mexico 34:203-206
Osteology
  Comparative, and myology, Iguanidae 37:35-56
  Cranial, *Sceloporus* 34:1-41
Otostigmus
  burgeri ***monsonus*** 17:30-41
  lavanus 17:30-41
  mesethus 17:30-41
  parvior 17:30-41
Otus asio, food habits
  Southeastern Oregon 46:421-426
Ovis
  canadensis
    Bone chewing by 50:89
    Northern Sierra Nevada, California 33:221-224
    Transferrin polymorphism, Colorado 40:141-142
  canadensis canadensis
    Epiphyseal fusion 47:7-12
Owls
  Barn
    Diet, Antelope Island, Great Salt Lake 46:307-309
    Seasonal food habits, Utah 32:229-234
    Sexual imprinting on humans 36:385-386
  Burrowing
    Food habits, Southeastern Idaho 39:274-276
    Food habits, Southeastern Oregon 46:421-426
    Foods, Conata Basin, South Dakota 45:287-290
    Nesting success, Southeastern Idaho 45:81-84
  Flammulated
    Capturing and monitoring 44:49-51
  Screech
    Food habits, Southeastern Oregon 46:421-426
    Winter food, Central Utah 31:83-84
  Spotted
    Bats in pellets, Southern Arizona 50:197-200
Ox, musk
  Pleistocene, systematics, Southeastern Idaho 47:239-251
Oxygen, low concentrations
  Aquatic insect tolerance 34:45-59
Oxytropis
  arctica ***barnebyana*** 28:147-156
  borealis ***australis*** 50:355-360
  campestris ***wanapum*** 50:373-377
  oreophila ***juniperina*** 38:225-367
  sericea, soil-site relationships
    Raft River Mountains, Utah 49:419-424

P

Pachycotes ***minor*** 45:266-275
Paddlefish parasites
  Yellowstone River, Montana 35:425-426
Paenoppia forficula 25:59-62
Pahranagat Valley, Nevada
  Cattle impact on fish populations 49:491-495
Palisades Creek, Idaho
  Cutthroat trout food size selection 45:327-331
Palm, Tertiary, systematics
  Dipping Vat Formation, Central Utah 32:1-15
Palmoxylon
  colei 33:61-76
  contortum 33:61-76
  edenense 33:61-76
  gustavesonii 32:1-15
Panama, rodent-infesting Anoplura 32:121-136
Panamint Valley, California
  Dipodomys merriami, burrowing habits 31:190-192
Pandeleteius ***bryanti*** 14:73-78
Parabacillus coloradus, life history 19:83
Paracarinolidia
  glabra 49:92-95
  longiseta 49:92-95
Paracoenia
  ampla 35:65-85
  calida 35:65-85
  wirthi 35:65-85
Paracopium ***gigantos*** 14:1-10
Paracorthylus velutinus 28:1-15
Paragordius
  Infection of immature aquatic insects 29:44
Paraiulus
  schmidti 12:13-34
  viganus 12:13-34
Paralidia
  bispinosa 46:329-335
  denticulata 46:329-335
  retrorsa 46:329-335
  singularis 46:329-335
  spinata 46:329-335
Paraphauloppia ***cordylinosa*** 35:103-108
Paraphyllanthoxylong ***utahense*** 43:394-402
Parasites
  Balaena mysticetus 47:355-372
  Brown trout, Montana 35:442-448
  Endemic fishes, Virgin River, Utah 46:662-676
  Helminth
    Cats and dogs, Central Utah 36:471-474
    Spermophilus elegans 47:103-104
    White-tailed jackrabbit, Colorado-Wyoming 45:604-606
  Indochinese refugees, Utah County, Utah 41:201-206

  Mottled sculpin, Utah 47:13-21
  Woundfin minnow, Virgin River, Utah 46:662-676
  Yellowstone Lake, Wyoming
    Cutthroat trout and longnose suckers 47:259-275
Parisuctobelba septenia 36:496-500
Parry, Charles Christopher 48:9-18
Partridge, Gray
  Foraging ecology, Eastern South Dakota 48:202-205
Paruroctonus boreus
  Biology and ecology 34:167-179
  Stinger utilization and predation 40:193-195
Paspalum
  distichum 42:101-104
  distichum indutum 42:101-104
Passalozetes
  linearis 22:93-100
  moniles 35:103-108
Paunsagunt Plateau, Utah
  Fire history 48:58-63
  Mammals 26:43-44
Paurodontus (Nematoda) 2:37-85
  apiticus 2:37-85
  densus 2:37-85
  gracilis 2:37-85
  niger 2:37-85
Peat, depth and profile changes, California 36:101-107
Pedicia
  ampla ***cinereicolor*** 18:31-36
  ampla ***perangusta*** 18:31-36
  bellamyana 24:117-122
  hynesiana 21:10-16
  pahasapa 18:31-36
  shastensis 18:31-36
  steensensis 18:31-36
Pediciaaspidoptera ***convexa*** 18:31-36
Pediocactus ***despainii*** 40:78-88
Pediomelum aromaticum ***tuhyi*** 46:254-260
Pelecyphorus semilaevis 22:110-113
Pelicans, American White
  Nesting colonies, Wyoming 48:285-289
Peloptulus ***tanytrichosus*** 32:208-210
Penicillidia ***godivae*** 24:107-115
Penstemon
  albifluvis 42:367-368
  angustifolius ***dulcis*** 46:459-460
  atwoodii 35:377-378
  eatonii and *Penstemon cyananthus*
    Comparative floral biology 40:268-272
  flowersii 43:429-431
  holmgrenii 37:100; 37:258
  idahoensis 48:495-498
  leonardii ***higginsii*** 46:459-460
  pseudospectabilis
    Mixed pollination systems 48:489-494
  scariosus ***cyanomontanus*** 46:459-460
  Systematics 35:434
    United States 34:311
  thompsonae ***desperatus*** 46:459-460
  thurberi ***anestius*** 34:230
Perca flavescens, parasites
  Deer Creek Reservoir, Utah 31:169-176
Perch, yellow, parasites
  Deer Creek Reservoir, Utah 31:169-176
Perdix perdix
  Foraging ecology, Eastern South Dakota 48:202-205
Peridryocoetes (Coleoptera) 44:223-230
Periphyton, composition and abundance
  Convict Creek, Sierra Nevada 46:595-611
Perissonemia ***ecmeles*** 21:108-113
Perityle ***specuicola*** 43:373-374
Perognathus
  longimembris
    Dominance relationships with *Microdipodops megacephalus* 34:312-316
    Nevada habitat invasion 29:143-149
  parvus, distribution, systematics, Utah 18:26-30
  Reproduction, Bonneville Basin, Utah 50:361-365
Peromyscus
  Fungi in the diet 47:308-313
  maniculatus
    Altitudinal hemoglobin variation 39:192-194
    Cuterebra larvae parasites 38:51-54
    Fleas, Colorado 43:168-174
    Genetic variation, Great Basin 46:577-580
    Short-term effects of logging on 40:183-189
    Subspecies ecology and taxonomy, Idaho 38:469-472
  Parasitized by botfly larvae
    Northern Colorado 36:481-482
  truei
    Cuterebra larvae parasites 38:51-54
    North Central Nevada, distribution 44:428-430
Perspinolidia peruviensis 49:96-99
Petropedes santarosae 32:176-179
Phacelia
  crenulata ***angustifolia*** 35:127-190
  demissa ***minor*** 46:254-260
  Systematics, keys, North America 35:127-190
Phalacrocorax auritus auritus
  Breeding biology, Utah 37:1-23
Phalacropsis dispar
  Control of native pine stem rust fungi 42:369-379
Phalacropsylla
  hamata, female 42:96-99
  morlani 42:241-245
Phalangida, ecology, Nevada Test Site 25:37-38
Phalaropes, Red-necked
  Migration biology, Great Basin 46:185-197
Phalaropus lobatus
  Migration biology, Great Basin 46:185-197
Phallorthus columbianus 12:13-34
Pheasants, Ring-necked
  Behavior in late winter, Central Utah 42:562-566
  Nest site selection, Utah 41:457-460
  Overwinter survival, Utah 41:247-250
Phenology, seasonal, *Nymphalis antiopa* 46:112-116

- *Phigalia plumogeraria*
  - Bionomics and control on bitterbrush, Utah 41:290-297
- *Philanthus*, nests and prey, Wyoming 26:35-40
- *Phloeocleptus*
  - ***ardis*** 41:121-128
  - ***atkinsoni*** 41:121-128
  - ***cristatus*** 41:121-128
  - ***punctatus*** 40:353-358
  - ***spicatus*** 41:121-128
- ***Phloeocurus*** (Coleoptera) 44:223-230
- ***Phloeographus mamibiae*** 44:223-230
- *Phloeosinopsoides* ***pumilus*** 45:266-275
- *Phloeosinus* ***phoebe*** 48:196-201
- ***Phloeoterus burserae*** 44:113-119
- *Phloeotribus*
  - ***amplus*** 37:383-394
  - ***destructor*** 29:113-128
  - ***fici*** 37:383-394
  - ***furvus*** 29:113-128
  - ***geminus*** 43:647-659
  - ***hirtus*** 37:383-394
  - ***ingae*** 37:383-394
  - ***levis*** 37:383-394
  - ***minor*** 37:383-394
  - ***nebulosus*** 37:383-394
  - ***perniciosus*** 42:223-231
  - ***quercinus*** 29:113-128
  - ***remorsus*** 37:383-394
  - ***simplex*** 27:79-97
  - ***simplicidens*** 37:383-394
  - ***squamiger*** 37:383-394
  - ***tetricus*** 37:383-394
  - ***vesculus*** 37:383-394
- *Phlox*
  - *austromontana* ***lutescens*** 45:791-792
  - *bryoides*, bee visitation 39:197-198
  - *longifolia*, systematics 39:1-14
- *Phragmites australis*
  - Diatoms on living and dead stems 40:223-228
- *Phrynosoma*
  - *douglassi*
    - Activity patterns, thermal ecology, Southeastern Idaho 45:607-614
  - *douglassii ornatum*
    - Notes on birth and growth 3:60
- Phycomycetes, aquatic, Lily Lake, Utah 32:181-189
- *Phyllolabis* ***hurdi*** 24:117-122
- *Phyllorhynchus decurtatus* ***porelli*** 34:241-244
- *Phyllotrox* ***canyonaceris*** 36:463-466
- *Physa zionis*
  - Zion National Park, Utah, distribution 46:310-315
- *Physaria*
  - *acutifolia* ***purpurea*** 37:279-365
  - *chambersii* ***sobolifera*** 46:254-260
  - Systematics, keys, Utah 33:31-36
- *Pica*
  - *pica*
    - Distribution and abundance, North America 35:269-272; 36:111
  - *pica hudsonia*
    - Predation on small mammals 45:152-153
- *Picea pungens*
  - *Chrysomyxa pirolata* on, Utah 42:262-272
- Piceance Basin, Colorado
  - Presettlement vegetation 43:687-699
  - Small mammal summer food habits 44:145-150
- Pikas
  - Blood protein, interpopulational variations 37:77-80
  - Marmot scats as winter food supplement 49:466-468
- Pine Butte Fen, Montana, vegetation and flora 46:22-32
- Pines
  - Bristlecone
    - Clark's Nutcracker interaction, White Mountains, California 44:357-360
    - Ecology, Utah and Eastern Nevada 44:487-494
    - Germination, Colorado 32:235-237
  - Limber, terminal bud formation 40:190-192
  - Lodgepole
    - Comparative successional roles, Southern Rocky Mountains 43:447-455
    - Effects of thinning 42:512-516
  - Mugo, cone spittlebug in Idaho 44:338-348
  - *Pisolithus tinctorius* association, acid mine spoils Sierra Nevada 49:111-112
  - Ponderosa
    - Conelet and cone mortality, Central Arizona 46:445-448
    - Disjunct stand, Southeastern Oregon 47:163-167
    - Insect damage and crown levels 44:575-578
    - Mortality by dwarf mistletoe-pandora moth, Arizona 45:432-426
    - Overstory influence on forage quality 48:78-82
    - Seeds, number and condition, Central Arizona 46:449-451
    - Site potential estimation, Southwestern United States 47:467-472
  - Western white, cone production
    - Mountain pine cone beetle population levels 44:310-312
- *Pinus*
  - *aristata*, germination, Colorado 32:235-237
  - *contorta*, effects of thinning 42:512-516
  - *edulis*, self-pollination 40:265-267
  - *flexilis*, effectiveness of seed dispersal 45:318-320
  - Hybrid stands, Northern Utah 32:171-175
  - *longaeva*
    - Ecology, Utah and Eastern Nevada 44:487-494
  - *monophylla*, seed, cone insects
    - Raft River Mountains, Utah 44:349-356
  - *ponderosa*, distributional aspects
    - Northwestern Nebraska 28:24-29
- Pinyon
  - Relict hybrid stands in Northern Utah 32:171-175
  - Singleleaf
    - Phytomass, regression methods for predicting

48:39-45

- Woodlands, monoterpene concentration in litter and soil 48:228-231

Pinyon-juniper
- Chaining, effect on browse species, Utah 46:508-512
- Small mammal summer food habits
  - Colorado 44:145-150
- Soil fungi beneath and between canopies
  - New Mexico 50:167-172
- Understory response to harvesting
  - Great Basin 45:105-112
- Understory vegetation, Nevada 41:467-475
- Woodlands
  - Densities, California and Nevada 46:178-184
  - Foliage biomass and cover, succession 50:121-134
  - Mature, plant community changes 47:96-99
  - Rodent weights, Southwestern New Mexico 48:554-557
  - Seed rain 46:706-710
  - Spatial pattern and interference, Northwestern Colorado 50:313-320
  - Succession following wildfire
    - Great Basin 45:556-566

Pisces, *Notolepidomyzon*, systematics 3:27-32

Pisidium variable, attack of trout 14:23-25

Pisolithus tinctorius
- Ectomycorrhizal formation on *Quercus*
  - Sierra Nevada minesoil 50:367-370
- Formation on California white fir
  - Sierra Nevada 50:85-87
- Pine associations, acid mine spoils
  - Sierra Nevada 49:111-112

Pityoborus
- ***hirtellus*** 18:46-56
- ***intonsus*** 18:46-56
- ***rubentis*** 18:46-56
- ***velutinus*** 18:46-56

Pityogenes ***mexicanus*** 40:353-358

Pityokteines ***mystacinus*** 35:21-32

Pityophthorus
- ***abiegnus*** 24:59-70
- ***ablusus*** 45:476-482
- ***abstrusus*** 36:425-444
- ***alnicolens*** 37:207-220
- ***amiculus*** 35:391-401
- ***anthracinus*** 36:425-444
- ***arcanus*** 36:425-444
- ***assitus*** 37:207-220
- ***atkinsoni*** 45:467-475
- ***atomus*** 24:59-70
- ***borrichiae*** 24:59-70
- ***bravoi*** 46:679-684
- ***brevicomatus*** 36:425-444
- ***burserae*** 36:347-365
- ***carinatus*** 38:71-84
- ***cavatus*** 38:71-84
- ***cedri*** 49:167-185
- ***chilgoza*** 49:167-185
- ***concinnus*** 37:207-220
- ***conscriptus*** 46:679-684
- ***conspectus*** 36:347-365
- ***corruptus*** 36:347-365
- ***costabilis*** 36:347-365
- ***costatulus*** 36:347-365
- ***costatus*** 35:391-401
- ***costifera*** 45:476-482
- ***cracentis*** 45:476-482
- ***cristatus*** 24:59-70
- ***crotonis*** 37:511-522
- ***debilis*** 36:347-365
- ***degener*** 35:391-401
- ***delicatus*** 38:397-405
- ***desultorius*** 45:476-482
- ***detentus*** 36:347-365
- ***diligens*** 36:347-365
- ***dimunitivus*** 45:467-475
- ***discretus*** 37:383-394
- ***dispar*** 36:425-444
- ***dissolutus*** 35:391-401
- ***dolus*** 24:59-70
- ***elatinus*** 24:59-70
- ***elimatus*** 36:425-444
- ***equihuai*** 45:467-475
- ***euterpes*** 38:71-84
- ***explicitus*** 35:391-401
- ***festus*** 27:36-57
- ***foratus*** 27:36-57
- ***franseriae*** 31:69-76
- ***furnissi*** 36:425-444
- ***galeritus*** 36:347-365
- ***germanus*** 36:425-444
- ***glutae*** 49:167-185
- ***hermosus*** 36:347-365
- ***hesperius*** 38:71-84
- ***hylocuroides*** 24:59-70
- ***impexus*** 38:71-84
- ***inceptis*** 35:391-401
- ***indefessus*** 46:641-645
- ***indigens*** 36:347-365; 37:207-220
- ***ineditus*** 36:425-444
- ***inhabilis*** 46:641-645
- ***inops*** 36:347-365
- ***insuetus*** 45:476-482
- ***intentus*** 38:71-84
- ***islasi*** 22:76-82
- ***laetus*** 36:347-365
- ***laticeps*** 38:71-84
- ***leechi*** 37:207-220
- ***lenis*** 36:347-365
- ***levis*** 46:265-273
- ***limatus*** 24:59-70
- ***litos*** 36:425-444
- ***malleatus*** 38:71-84
- ***medialis*** 36:347-365
- ***megas*** 36:425-444
- ***melanurus*** 36:347-365
- ***mendosus*** 35:391-401

  mesembria 38:71-84
  minus 36:425-444
  minutalis 36:347-365
  molestus 36:347-365
  montezumae 38:71-84
  morosus 36:347-365
  nanus 24:59-70
  nebulosus 36:347-365
  nemoralis 36:347-365
  nugalis 36:347-365
  occlusus 36:425-444
  ostryacolens 46:679-684
  paulus 24:59-70
  perexiguus 36:347-365
  pusillus 24:59-70
  quercinus 27:36-57
  recans 36:425-444
  rubidus 38:397-405
  scalptus 38:71-84
  scitulus 36:347-365
  siouxensis 36:425-444
  sobrinus 36:347-365
  solatus 37:207-220
  speciosus 37:207-220
  speculum 36:425-444
  strictus 36:347-365
  subimpressus 36:425-444
  tenax 36:347-365
  thamnus 45:467-475
  thatcheri 36:425-444
  thomasi 36:425-444
  timidulus 35:391-401
  toralis 24:59-70
  torridus 31:69-76
  trepidus 38:71-84
  trunculus 45:467-475
  tutulus 46:641-645
  vegrandis 46:641-645
  vesculus 38:397-405
  vespertinus 38:71-84
  zexmenivora 45:467-475
  zonalis 36:425-444
Plagiobothrys, systematics, keys 34:161-166
Plagiostira
  gillettei utahensis 22:105-107
  mescaleroensis 20:39-47
Plagopterus argentissimus
  Biology, Virgin River Basin 38:463-468
  Parasites, Virgin River, Utah 46:662-676
  Spawning and growth 42:549-552
Plague, fleas in pine martens 44:170-175
Plant communities
  Alpine, Kings Peak, Uinta Mountains, Utah 42:50-59
  Changes in mature pinyon-juniper woodland 47:96-99
  Foothill knolls, Uinta Basin, Utah 42:81-90
  Lake Gilbert, Nevada 46:1-21
  Navajo National Monument, Arizona 45:1-13
  Pluvial lake basin, Lake Gilbert, Nevada 46:1-21
  Spring denitrification rates
    Sierra Nevada 48:558-562
  Understory and open-area differentiation 40:167-174
  Variability, Southeastern Montana 43:660-668
  Wetland, Uinta Mountains, Utah 43:523-530
  Zonation
    Benton Hot Springs, California 47:583-591
    Saline meadow, Utah Lake 47:322-333
Plant species diversity
  Soil texture in grasslands, Eastern Great Basin 33:163-168
Plant-animal interactions
  Nectar-sugar concentrations and visitors 37:523-529
Plants
  Alien, Southern Idaho, invasion in 1900 41:176-183
  C3 and C4, ecological differences
    Central Utah 46:140-147
  Chemical composition
    Related to mule deer reproduction 39:122-128
  Chromosome counts, Western America 33:19-25
  Desert, symbiotic nitrogen fixation 36:65-80
  Endangered and threatened, Utah 38:1-18
  Fossil, ultrastructure, Eocene, India 41:161-166
  Names, index of authors, Utah 42:385-394
  Nutrient levels on summer ranges
    River of No Return Wilderness Area, Idaho 44:621-626
  Poisonous, Utah, checklist 40:229-253
  Rare, Colorado 48:434-484
  Subalpine herbaceous
    Reproduction, Wasatch Mountains, Utah 43:573-578
  Utah, rare 45:173-236
  Vascular
    Angel Island, Marin County, California, checklist 40:385-407
    Bighorn Canyon, Wyoming-Montana, checklist 45:734-746
    Bryce Canyon National Park, Utah, checklist 41:109-120
    Canyon and Church Mountains, Utah, checklist 44:277-295
    Colorado, distributional records 38:208-210
    House Range, Utah, checklist 48:102-116
    Kaiparowits Basin, checklist 38:125-179
    Lee Creek Valley, Alberta, checklist 39:277-283
    Navajo National Monument, checklist 38:19-30
    Rare, Idaho National Engineering Laboratory 44:140-144
    San Rafael Swell, Utah, checklist 43:79-87
    Special status, Utah, checklist 35:327-376
    Systematics, Utah 42:129-195; 46:254-260; 46:261-264
    Teton County, Wyoming, checklist 40:408-413
    Upper Walker River, California and Nevada, checklist 43:93-130
    Utah, checklist 41:1-108

  Zonation and climate, Late Quaternary
    Southeastern Utah 44:1-35
Plapigella ***jessicae*** 49:398-403
Platydesmus
  calus 12:13-34
  crucis 12:13-34
  excisus 12:13-34
  perditus 12:13-34
Platyoplus gilaensis 33:43-50
Platypus
  abditulus 26:45-70
  abietis 18:37-40
  angustatulus 26:45-70
  annexus 26:45-70
  applanatus 31:243-253
  brevicornis 26:45-70
  chiriquensis 26:45-70
  clunalis 26:45-70
  cluniculus 26:45-70
  clunis 26:45-70
  connexus 26:45-70
  deceptor 31:243-253
  deplanatus 31:243-253
  eugestus 26:45-70
  eversus 31:243-253
  eximius 31:243-253
  exitialis 26:45-70
  filaris 31:243-253
  liraticus 26:45-70
  longior 26:45-70
  longius 26:45-70
  nudatus 31:243-253
  occipitis 26:45-70
  pouteriae 31:243-253
  prenexus 26:45-70
  quadridentatus 31:243-253
  querceus 31:243-253
  schedli 26:45-70
  secus 31:243-253
  senexus 26:45-70
  sicarius 31:243-253
  simpliciformis 26:45-70
  spectus 31:243-253
  vegestus 26:45-70
Plecoptera
  Capnia, systematics, distribution, keys
    North America 49:289-363
  Chloroperlidae
    Systematics, Nearctic Region 41:349-359
  Distribution, New Mexico 43:585-591
  Distributional records, Nevada and Utah 39:289-292
  Hesperoperla, systematics, California 40:63-67
  Isoperla, systematics, Nearctic Region 36:211-220
  Neoperla, systematics, Nearctic Region 38:97-114
  Nevada, checklist 35:49-50
  New Mexico, checklist 35:97-99
  North America
    Checklist, distribution, bibliography 46:383-397
  Nymph growth, constant high temperatures 35:51-61
  Perlidae, systematics 34:83-93
  Perlodinae nymphs
    Systematics, keys, North America 44:373-415
  Soliperla
    Systematics, keys, Nearctic Region 43:30-44
  Southeastern Idaho, checklist 36:501-504
  Systematics, keys, Louisiana 36:366-384
  Systematics, Utah 33:91-108
Pleistocene
  Trumpeter Swan, Utah 46:547-548
  Utah, *Gila atraria* 49:131-133
Pleistocene, Late
  Canids, Utah 46:415-420
  Coniferous woodlands
    Lucerne Valley, California 36:227-238
  Fauna, Snake Creek Burial Cave 49:143-154
  Mammals
    Little Box Elder Cave, Wyoming 31:93-105
Plesionema ***eteosa*** 14:1-10
Pnigodes
  buchanani 4:1-38
  tuberosus 4:1-38
Poa, systematics, keys, Rocky Mountains 45:395-422
Poaceae
  Elymus simplex
    Systematics, Colorado and Wyoming 36:239-241
  Paspalum, systematics, United States 42:101-104
  Poa, systematics, keys, Rocky Mountains 45:395-422
Poecilanthrax
  alpha ***zionensis*** 17:1-26
  butleri 17:1-26
  colei 17:1-26
  fasciatus 17:1-26
  ingens 17:1-26
  marginatus 17:1-26
  marmoreus 17:1-26
  robustus 17:1-26
  sackenii ***monticola*** 17:1-26
Poeciliopsis occidentalis occidentalis
  Management, Bylas Springs, Arizona 50:265-273
Pogonomyrmex occidentalis
  Prairie dog diggings in mounds of, Utah 49:36-37
  Swarming 40:165-166
Pokabius ***aethes*** 11:115-118
Polemoniaceae
  Gilia, systematics, keys, Utah 49:461-465
  Phlox
    Systematics, Utah 45:791-792
    Systematics, keys, North America 39:1-14
Polites sabuleti
  Genetics, environment, and systematics 35:33-38
Pollen grain germination
  Torenia asiatica, chemical effects on 34:71-81
Pollination, mixed systems
  Penstemon pseudospectabilis 48:489-494
Polygonaceae
  Eriogonum

    Systematics 32:113-116; 40:143-148
    Systematics, Intermountain Region 34:245-246
    Systematics, keys 27:183-229; 36:281-333
    Systematics, keys, Nevada 45:493-519
    Systematics, Nevada 45:276-280
    Systematics, Southern Nevada 28:157-159
    Systematics, types, Nevada 45:488-492
    Systematics, Utah 41:229-231
    Systematics, Western Colorado 33:120-122
  Eriogonum pauciflorum
    Systematics, keys 27:102-117
  Stenogonum, systematics 36:272-280
  Systematics, Argentina 41:143-146
  Systematics, keys, Utah 44:519-557
Polygraphus
  anogeissi 48:188-195
  difficilis 48:188-195
  querci 48:188-195
Polymorphism, *Mimulus guttatus* 43:470-474
Polyodon spathula
  Parasites of, Yellowstone River, Montana 35:425-426
Populus tremuloides
  Castor canadensis foraging in Central Utah 48:250-262
  Long-term effects of 2,4-D treatment 44:459-467
Portulaceae, *Talinum*, systematics, Utah 45:485-487
Posthodiplostomum minimum
  Host-induced morphological variations 37:129-137; 37:375-382; 37:481-488
  Host-parasite relationships 36:334-346
Potholes
  Zonation patterns, Kalsow Prairie, Iowa 40:372-384
Power plants, warm water aquaculture 44:75-82
Prairie, shortgrass
  Spatiotemporal variation in floral resources 40:197-215
Prairie, tall-grass
  Species, ecology, Kalsow Prairie, Iowa 43:137-167
Prairie Chicken, Lesser
  Nest site selection and vegetation characteristics, Texas 49:624-626
Prairie dogs
  Black-tailed
    Ecology, associated species, Western South Dakota 50:339-345
    Livestock grazing 46:198-203
    Mound architecture 49:621-623
    Populations one year after rodenticides 50:107-113
    Reproductive ecology, Montana 47:202-206
    Rodenticide-treated site reoccupation 47:339-343
  Burrow plugging and Siberian polecats 44:447-449
  Burrows, Hutton Lake National Wildlife Refuge, Wyoming 31:115-124
  Colony attributes and associated vertebrates 42:572-582
  Utah
    Burrowing and denning, captive colony 44:495-498
    Reestablishment, Capitol Reef National Park, Utah 42:517-523
  White-tailed
    Burrow structure and function 49:517-524
    Diggings in western harvester ant mounds, Utah 49:36-37
Presettlement landscapes
  Using land survey notes to reconstruct 50:181-191
Primula ***domensis*** 45:548-550
Primulaceae, *Primula*, systematics, Utah 45:548-550
Prionocera ***broweriana*** 21:79-86
Prionosceles
  glaber 21:87-107
  panamensis 21:87-107
Procryphalus mucronatus, bionomics 37:105-127
Prosopis velutina
  Casa Grande National Monument, Arizona 31:153-159
Prostemmiulus
  atypus 12:13-34
  obscurus 12:13-34
Protocedroxylon ***macgregorii*** 46:452-458
Protohylastes annosus 33:77-90
Protopinaceae
  Protocedroxylon, systematics 46:452-458
Protoplatypus vetulus 33:77-90
Provo River, Utah
  Macroinvertebrates, checklist 32:211-219
Prunus nigra, Alberta, Canada
  Misidentification of *Rhamnus cathartica* 38:123
Pseudobryobia ***knowltoni*** 36:57-64
Pseudochramesus ***jaliscoensis*** 47:547-550
Pseudoeucyllus boulderensis 10:71-73
Pseudogekko ***shebae*** 9:41-45
Pseudohylesinus ***pini*** 29:113-128
Pseudopityophthorus
  denticulus 37:207-220
  durangoensis 47:547-550
  granulifer 27:36-57
  hondurensis 27:36-57
  micans 27:36-57
  peregrinus 46:461-464
  tenuis 19:1-7
  tropicalis 27:36-57
  xalapae 47:547-550
Pseudoscorpions
  Heterosphyronid, systematics, New Mexico 12:39-45
Pseudothysanoes
  atomus 40:353-358
  brunneus 31:69-76
  concentralis 35:21-32
  fimbriatus 42:223-231
  frondicolens 31:69-76
  leechi 40:353-358
  mandibularis 44:113-119
  multispinatus 17:105-110
  perseae 41:121-128
  pini 42:223-231
  securus 37:207-220
  spinura 19:57-62

  squameus 44:113-119
  thomasi 27:36-57
  tumidulus 35:21-32
  turnbowi 37:207-220
Pseudotremia
  fracta 11:19-26
  hansoni 11:19-26
Pseudotsuga menziesii
  Dendroctonus pseudotsugae broods on 48:348-351
  Growth variation, Central Utah 39:219-225
  Rhabdocline needle blight 41:476-477
Pseudoxylechinus (Coleoptera) 46:465-467
  indicus 46:468
  rugatus 46:465-467
  sinensis 46:465-467
  tibetensis 46:465-467
  uniformis 46:465-467
  variegatus 46:465-467
Psoralea
  lanceolata, systematics, keys 32:76-87
  pariensis 35:327-376
Ptarmigan, Rock
  Foods and weights, Amchitka, Aleutian Islands, Alaska 48:533-540
Pteichocheilius lucius
  Ophiotaenia parasites 41:445-448
Pteronarcys californica
  Detrital processing 46:33-38
  Occurrence and distribution within streams 33:218-220
  Sexual dimorphism in malpighian tubules 35:449-451
Ptychocheilus lucius, life strategies 46:656-661
Pulmonata, *Triodopsis cragini*, type locality 14:87-89
Pupfish
  Amargosa
    Systematics, Ash Meadows, Nevada 46:220-223
  Behavior in differing environments 29:169-180
  Devil's Hole
    Daily and yearly movement 43:592-596
  Salt Creek
    Adapting to fresh water 41:341-342
Purshia tridentata
  Impact of 1975 Wallsburg, Utah fire 40:299-302
Pycnarthrum
  amersum 43:647-659
  fulgidum 37:207-220
Pygmaelidia bullata 48:232-249
Pyramid Lake, Nevada
  Catostomus tahoensis
    Reproductive ecology 38:181-186
  Cui-ui, life history 45:571-603
  Fish species composition and abundance 41:395-408
  Gila bicolor
    Reproductive biology 38:203-207
    Seasonal growth 43:713-716
  Larval tui chubs, food 43:175-178
  Sacramento perch, life history 41:278-289
  Salmo clarki henshawi, life history 43:1-29
  Vertical distribution of adult fish 38:417-428

Q

Quadraseta
  falconensis 37:501-509
  mirandae 37:501-509
  rotstieri 37:501-509
  tachirensis 37:501-509
Quaternary, Late
  Southeastern Utah plant zonation and climate 44:1-35
Quercus
  gambelii
    Recovery after fire 40:127-130
    Utah 41:147-153
  gambelii ***bonina*** 46:107-111
  havardii ***tuckeri*** 46:107-111
  Systematics, Utah 41:147-153
Quiscalus mexicanus
  Nesting record, Nevada 45:483-484

R

Rabbitbrush, white rubber
    Photosynthesis, high rates 45:520-526
Rabbits
  Pygmy
    Alarm call 41:158-160
    Colorado River drainage 47:231-233
    Homing 39:88
    Oregon, habitat and distribution 44:563-571
Raccoons, Wyoming, distribution 42:599-600
Radiation
  Background
    Southern Colorado endemic fauna 19:37-42
  Effects on *Tradescantia*
    Uranium mill tailings 38:456-462
Radio transmitter
  Attachment on Chukars 49:632-636
    Effect on mating 50:379-380
  Implants, wild canids 45:567-570
Radioactive waste dispersion
  Small mammals, Idaho 46:404-410
Raft River Mountains, Utah
  White locoweed soil-site relationships 49:419-424
Rana pretiosa pretiosa
  Ecology and life history 29:45-81
Range fire, post fire insect comparisons 46:721-727
Ranunculus testiculatus
  Allelopathic effects on grasses and forbs 38:90-96
Raptors
  Breeding
    Food habits, nest characteristics, Southwestern Wyoming 48:548-553
  Manti-La Sal National Forest, survey 39:155-160
  Mortality, Western Utah 29:165-167
  Nest site selection
    Eastern Great Basin Desert 42:395-404

  - Nesting, Curlew Valley, Utah 31:51-65
  - Uinta National Forest, Utah 38:438-446
- Rasmussen, Andrew T. 15:50-54
- Rattlesnakes
  - Cannibalism, Lethbridge, Canada 31:49-50
  - Western diamondback
    - Nevada occurrence doubtful 42:350
- Raven, Common
  - Nesting on interstate highway overpasses 48:64-67
  - Unusual social feeding and soaring 45:150-151
- Reclamation
  - Coal mine spoils in the Southwest 44:441-446
- Regression analysis
  - Methods
    - Biomass estimation, sagebrush and bunchgrass 49:373-380
    - Predicting singleleaf pinyon phytomass 48:39-45
  - Sagebrush-grass biomass prediction 45:94-98
- *Reithrodontomys megalotis megalotis*
  - Growth and development 34:105-120
- *Relictus solitarius*
  - Temperature and salinity relationships 42:541-548
- Reptiles
  - Buccal floor, summary 42:273-349
  - BYU and U. of U. collections 26:87-135
  - Chihuahua, Mexico 19:75-82
  - *Crotaphytus*, systematics 23:129-148
  - Death Valley, California 23:119-128
  - Extant, indigenous population
    - Baja California Sur 49:496-502
  - Fossil, *Cathetosaurus*, systematics 48:121-145
  - *Hypsiglena*
    - Systematics 5:25-92
    - Systematics, Sonora, Mexico 41:139-142
    - Systematics, Western North America 4:49-54
  - Idaho
    - Checklist 2:87-97
    - Richard P. Erwin collections 44:111-112
  - Nevada Test Site 29:31-34; 42:219-222
  - New Mexico 9:55-57
  - Population changes
    - Sonoran Desert shrub 41:129-138
  - *Pseudogekko*, systematics, Solomon Islands 9:41-45
  - Responses to land management 39:255-262
  - Systematics, Southern Mexico 17:52-56
  - *Thamnophis*
    - Systematics, Mexico and New Mexico 48:499-507
    - Systematics, North America 49:511-516
  - *Xerobates*
    - Systematics, Baja California Sur, Mexico 49:496-502
- Rhabdocline needle blight, Douglas-fir 41:476-477
- *Rhabdomastix*
  - ***hynesi*** 26:1-8
  - *neolurida* ***flaviventris*** 24:117-122
- *Rhagoletis pomonella*
  - Adaptation for cherries, Utah 46:173-174
- *Rhagovelia* ***culebrana*** 12:47-54
- *Rhamnus cathartica*, Alberta, Canada
  - Misidentified as *Prunus nigra* 38:123
- *Rhinoclemmys areolata*
  - Courtship behavior, Western Tabasco, Mexico 48:263-266
- *Rhizopalmoxylon*
  - ***behuninii*** 32:1-15
  - ***blackii*** 32:1-15
  - ***scottii*** 32:1-15
- *Rhopalomyia*
  - ***subhumilis*** 37:426-428
  - *subhumilis*, bionomics 37:429-442
- Rhynchophora
  - Female genitalia and spermathecae 20:1-22
- Ribulose diphosphate carboxylase activities
  - *Lycopersicon esculentum* 40:121-126
  - *Malva neglecta* 40:121-126
- Rillscale
  - Forage quality on amended bentonite mine spoil 50:57-62
- Rincon Mountains, Arizona
  - Desert shrew habitat, distribution 49:140-141
- River of No Return Wilderness Area, Idaho
  - Coyote summer food habits 50:63-65
  - Plant nutrient levels on summer ranges 44:621-626
- Riverbottom forest community
  - Taxonomic and ecological study, Alberta, Canada 36:243-271
- *Roccus chrysops*
  - Spawning ecology, Utah Lake 28:63-69
- Rock Island, Utah Lake, Utah
  - Water birds 6:127-128
- Rocky Mountain National Park, Colorado
  - *Peromyscus maniculatus* fleas 43:168-174
- Rocky Mountain spotted fever
  - Utah, vectors and hosts 14:31-37
- Rocky Mountains
  - Soil nematodes, genera and biomass 47:473-479
  - Western spruce budworm
    - Natural enemies 47:319-321
- Rocky Mountains, Southern
  - Trembling aspen and lodgepole pine, succession 43:447-455
- Rodenticides
  - *Cynomys ludovicianus* populations
    - One year after treatment 50:107-113
  - Prairie dog, effects on deer mice
    - Western South Dakota 50:347-353
- Rodents
  - Annual energy budgets
    - Northern Great Basin 39:143-154
  - Cold desert, harvester ant competition 39:267-273
  - Density and habitat
    - Shadscale and sagebrush 33:255-264
  - Desert, niche pattern, Great Basin 47:488-496
  - Ecological distribution
    - Canyonlands National Park, Utah 39:199-205
  - Geomyid, mima mounds, Oregon 47:609-619

- Microtine, ecology
  - Grand Teton National Park, Wyoming 33:205-217
- Movements of individuals
  - Central Nevada 29:109-110
- Populations in *Artemisia tridentata*, Utah 35:191-202
- Southern Utah
  - Experimental habitat manipulation and population 49:435-448
- Weights, pinyon-juniper woodlands
  - Southwestern New Mexico 48:554-557

- Rosaceae, systematics, keys, Utah 42:1-44
- Rotger Collection, Coleoptera, Carabidae 47:631-637
- Rubiaceae, *Galium*, systematics, Utah 37:510
- Ruby Lake, Nevada, small mammals 49:123-130
- Rush Valley, Utah
  - Rodent populations in *Artemisia tridentata* 35:191-202
- Ruth Reservoir, California
  - Fish distribution and abundance 42:529-540

S

- Sage Hens, road kills, Utah 7:30
- Sagebrush
  - Big
    - Control attempts 40:157-164
    - Leaf morphology of subspecies 35:325-326
    - Longleaf snowberry associations, Northeastern Nevada 47:117-131
    - Seed planting depth 47:497-499
    - Selection by Sage Grouse 48:274-279
  - Black
    - Nutritive content, winter 46:161-165
  - Community characteristics
    - Mountainous Northeastern Nevada 48:403-421
  - Community type classification, keys 48:422-433
  - Community types, soil characteristics
    - Mountainous Northeastern Nevada 49:469-481
  - Grazing impacts, Central Utah 41:335-340
  - Plains silver
    - Sprouting and seedling establishment 50:201-207
  - Regression methods for biomass estimation 49:373-380
  - Wilt disease of unknown cause, Utah 41:184-191
- Sagebrush-grass
  - Biomass predicted by regression 45:94-98
- Sagehen Creek Basin, California
  - Trichoptera species, emergence, habitat 49:186-197
- *Sahniocarpon harrisii* 47:527-535
- Salamanders
  - Clouded, food habits, Oregon 46:228-240
  - *Magnadigita*, systematics, Panama 21:23-26
  - Mass mortality by *Acinetobacter*
    - Wasatch Mountains, Utah 49:364-372
  - Plethodontid, systematics, Mexico 10:37-44
  - Tiger, life history
    - Chihuahuan Desert, New Mexico 31:193-212
- Saldidae, stridulatory organs 11:43-46
- *Saldula*
  - ***durangoana*** 32:137-153
  - ***saxicola*** 32:137-153
  - ***varionis*** 10:51-61
- Salicaceae, systematics, keys, Utah 43:531-550
- *Salicornia pacifica utahensis*
  - Salt content and environment 35:86-96
- Salientia, adaptations 7:11-15
- *Salmo*
  - *clarki*
    - Food size selection, Palisades Creek, Idaho 45:327-331
    - Parasites, Yellowstone Lake, Wyoming 47:259-275
    - Parasitized by *Trichophrya*, Yellowstone Lake, Wyoming 45:255-265
    - Western Bonneville Basin, subspecies status 38:193-202
  - *clarki henshawi*
    - Life history in Pyramid Lake, Nevada 43:1-29
  - *trutta*
    - Internal parasites, Montana 35:442-448
    - Water fertility and reproduction, Montana 35:435-441
- Salmon River, Middle Fork, Idaho
  - Diatoms, distribution and abundance 44:421-427
- Salmon, chinook, juvenile
  - Effects of artificial shading 47:22-31
- *Salsola*, seed dispersal in hybrids 41:370-376
- Saltbrush, fourwing, winter crude protein 41:343-346
- Saltcedar, habitat relationships, Central Utah 46:535-541
- *Salvelinus fontinalis*
  - Effects of watershed alteration 46:39-45
- *Salvia dorrii*, typification 41:198-200
- Sampling
  - Frequency, quadrat and sample sizes, mountain meadow vegetation 49:241-248
- San Juan County, New Mexico, birds 37:489-500
- San Juan Mountains, Colorado
  - Tundra vegetation 45:87-93
- San Luis Valley, Colorado
  - Background radiation and endemic fauna 19:37-42
- San Mateo County, California
  - Host-parasite relationships of ticks 24:1-6
- San Rafael Swell, Utah
  - Vascular flora, checklist 43:79-87
- Saratoga Springs, California
  - Lizards, environmental response 30:146-165
- *Sarcobatus vermiculatus*
  - Community ecology, Central Utah 46:348-357
  - Germination factors 47:110-116
- Sauria
  - *Brachylophus*
    - Systematics, Fiji and Tonga 30:166-172
  - *Crotaphytus*
    - Systematics 32:25-34
    - *wislizeni*, systematics, Baja California 28:183-194
- Saxifragaceae, systematics, keys, Utah 45:155-172
- Scale, San Jose

- Parasitized by *Aphytis vandenboschi*, Northern Utah 48:388-393

Scaphiopus
- *intermontanus*, Utah 45:22-30
- Systematics 1:3-25

Scaphiostreptus
- ***dybasi*** 12:13-34
- ***ergus*** 12:13-34
- ***simplex*** 12:13-34

Sceloporus
- *clarki* ***uriquensis*** 19:75-82
- Cranial osteology, numeric analysis 34:1-41
- *graciosus*
  - Aberrant karyotypes 46:224-227
  - Activity patterns, thermal ecology, Southeastern Idaho 45:607-614
- Helminths of, Utah 33:1-18
- *horridus*, feeding habits, Jalisco, Mexico 36:108-110
- *magister*
  - ***cephaloflavus*** 15:32-34
  - Ecology, Nevada Test Site 33:133-146
- *megalepidurus* ***halli*** 34:231-237
- *nelsoni* ***coeruleus*** 19:75-82
- *poinsettii* ***robisoni*** 47:383-421
- *scalaris* ***samcolemani*** 34:97-104

Schedlarius (Coleoptera) 17:103-104

Schizolachnus ***wahlea*** 12:57-61

Schizotetranychus ***agropyron*** 36:57-64

Schoolroom Glacier, Wyoming
- Alpine vegetation 43:483-491

Sciurus aberti
- Dorsal hair length and coat color 42:597-598
- Effects of logging on, Utah 47:252-258
- Post-Pleistocene dispersal, modern distribution 49:425-434

Sclerocactus
- ***blainei*** 45:553-555
- ***schlesseri*** 46:677-678

Scolytidae
- American, introduced and exported 37:67-74
- Checklist, Idaho 47:375-382

Scolytodes
- ***amabilis*** 35:21-32
- ***amoenus*** 27:119-141
- ***anceps*** 41:121-128
- ***canaliculus*** 37:511-522
- ***clusiacolens*** 27:119-141
- ***clusiavorus*** 27:119-141
- ***comitabilis*** 38:397-405
- ***constrictus*** 37:511-522
- ***contractus*** 37:511-522
- ***crinalis*** 38:397-405
- ***crinitus*** 38:397-405
- ***decorus*** 38:397-405
- ***facetus*** 27:119-141
- ***festus*** 37:511-522
- ***ficicolens*** 41:121-128
- ***ficivorus*** 27:119-141
- ***fulmineus*** 37:207-220
- ***genialis*** 35:21-32; 38:397-405
- ***habilis*** 38:397-405
- ***ingavorus*** 27:119-141
- ***jucundus*** 37:511-522
- ***lepidus*** 35:21-32
- ***libidus*** 38:397-405
- ***naevius*** 41:121-128
- ***nanellus*** 27:119-141
- ***obesus*** 35:21-32
- ***opacus*** 37:511-522
- ***opimus*** 37:511-522
- ***perditus*** 27:119-141
- ***perpussilus*** 38:397-405
- ***pilifer*** 42:223-231
- ***plumericolens*** 43:647-659
- ***praeceps*** 37:511-522
- ***proximus*** 27:119-141
- ***pusillimus*** 41:121-128
- ***radiatus*** 37:207-220
- ***retifer*** 43:647-659
- ***semipunctatus*** 38:397-405
- ***serenus*** 37:511-522
- ***suturalis*** 37:511-522
- ***tardus*** 41:121-128
- ***varius*** 37:511-522
- ***venustulus*** 27:119-141
- ***vesculus*** 41:121-128

Scolytogenes ***indicus*** 49:167-185

Scolytominus
- ***andamanensis*** 48:196-201
- ***mimusopis*** 48:196-201
- ***quadridens*** 48:196-201
- ***rectus*** 48:196-201

Scolytopsis
- ***cubensis*** 21:87-107
- ***laticollis*** 28:1-15

Scolytus
- ***aztecus*** 27:119-141
- ***binodus*** 42:223-231
- ***hermosus*** 28:1-15
- ***laetus*** 35:21-32
- ***mundus*** 28:1-15
- ***obelus*** 22:76-82
- ***torulus*** 35:21-32

Scoria rock outcrops, avian use 47:625-630

Scorpions
- National Reactor Testing Station, Idaho 33:251-254
- Northern, biology and ecology 34:167-179
- Systematics, keys, Utah 32:154-170

Scrophulariaceae
- *Mimulus*, systematics 36:81-85
- *Penstemon*
  - Systematics 35:434
  - Systematics, Idaho 48:495-498
  - Systematics, Nevada 34:230
  - Systematics, Uinta Basin 42:367-368; 43:429-431
  - Systematics, United States 34:311

    - Systematics, Utah 46:459-460
    - Systematics, Western United States 37:100; 37:258
- Sculpins
  - Distribution, Clearwater River Basin, Idaho 39:59-62
  - Morphometry
    - Clearwater drainage, Idaho 38:115-122
  - Shoshone, distribution
    - Hagerman Valley, Idaho 44:324-326
- Sedges, Nebraska, dry-year grazing 47:422-426
- Seed rain, pinyon-juniper woodlands 46:706-710
- Seeds
  - Dispersal
    - *Pinus flexilis* 45:318-320
    - *Salsola* hybrids 41:370-376
  - Germination
    - Dwarf mistletoe, forest smoke effects 47:652-659
    - *Mimulus guttatus* 43:470-474
  - Viability after long-term storage
    - Shrub and forb species 41:274-277
- Selenium, Nevada, soils, plants and animals 49:201-213
- SEM analysis
  - *Equisetum* stem morphology, Utah 48:51-57
- *Senecio* ***toiyabensis*** 40:78-88
- Sequoia National Park, California
  - *Carex exserta*, soil nutrients 45:61-66
- Sexual dimorphism, *Pteronarcys californica* 35:449-451
- *Shannonomyia* ***semireducta*** 30:232-241
- Sheep
  - Bighorn
    - Prehistoric, Northern Sierra Nevada, California 33:221-224
    - Transferrin polymorphism, Colorado 40:141-142
  - Haloxon and thiabendazole as anthelmintics 29:35-41
  - Rocky Mountain bighorn
    - Bone chewing by 50:89
    - Epiphyseal fusion 47:7-12
- Sheeprock Mountains, Utah
  - Blue Grouse winter habitats and foods 49:229-232
- Shivwits Plateau, Arizona
  - Avifauna of Mt. Dellenbaugh Region 41:259-268
- ***Shoshoniulus*** (Paraiulidae) 11:19-26
- Shredders
  - Leaf litter decomposition when excluded 46:204-207
- Shrew, desert
  - Habitat, distribution, Rincon Mountains, Arizona 49:140-141
- Shrub Research Consortium 44:182
- Shrubs
  - Desert phytomass and minerals
    - Curlew Valley, Utah 44:327-337
  - Electrophoresis of isoenzymes 41:377-388
  - Mountain habitats, Wyoming
    - Arthropod effects on root:shoot biomass 49:456-460
  - Seed viability, long-term storage 41:274-277
- *Sialia mexicana*, leucism 48:75-77
- Sierra Nevada
  - Periphyton and aquatic insects 46:595-611
  - *Pisolithus tinctorius*
    - Ectomycorrhizal formation on *Quercus* 50:367-370
    - Formation on California white fir 50:85-87
    - Pine association, acid mine spoils 49:111-112
  - Plant communities
    - Spring denitrification rates 48:558-562
- Sierra Nevada, Northern
  - Prehistoric bighorn sheep 33:221-224
- Silver Creek, Utah, Pleistocene vertebrates 36:387-424
- Simuliidae, systematics, keys, Utah 20:81-104
- Siphonaptera
  - Anomiopsyllinae
    - Systematics, keys, North America 39:351-418
  - *Meringis*, systematics, keys 38:447-455
  - Mesa Verde National Park, Colorado 26:76-78
  - *Phalacropsylla*, systematics, keys 42:96-99; 42:241-245
  - Systematics, Utah 11:105-114
  - Utah, distribution 10:62-65
  - Variations in Thomas wood rat nests 15:35-49
- *Siphonophora*
  - ***conicornis*** 12:13-34
  - *fallens* ***annecta*** 12:13-34
  - ***vera*** 12:13-34
- *Siren intermedia*
  - Authorship and date of publication 35:100-102
- *Sitanion hystrix*
  - Leaf anatomy and CO_2 assimilation 39:427-432
- *Sitona*
  - ***alpinensis*** 47:168-174
  - ***bryanti*** 47:168-174
  - ***oregonensis*** 47:168-174
- Skinks
  - Prairie
    - Bibliography and subject index 49:525-534
    - Influence of substrate water content on neonate size 49:198-200
    - Maternal care of neonates 47:536-537
    - Reproduction, Nebraska 47:373-374
  - Skilton's, life history, Utah 4:81-88
  - Systematics
    - Chihuahua, Mexico 17:111-117
    - Durango, Mexico 18:57-62
  - Western, ecology, systematics 17:59-94
- Slevin, Joseph Richard 17:56-58
- Smith, Rozella Pearl Beverly Blood 48:180-187
- Snake Creek Burial Cave
  - Quaternary mustelids 49:143-154
- Snake River Canyon, Wyoming
  - Bald Eagles 41:461-464
- Snakes
  - *Amastridium*
    - Systematics, Oaxaca, Mexico 31:254-255
  - Colubrid, Sonora, Mexico 26:136-140
  - Garter
    - Number, length, and weight of young 9:51-54
  - *Lichanura*, systematics, Mexico 38:411-416
  - Long-nosed, Idaho 36:56

Phyllorhynchus, systematics, Mexico 34:241-244
  Southwestern Idaho
    Distribution and abundance 41:154-157
  Systematics, distribution
    Baja California, Mexico 38:406-410
  Systematics, Western Chihuahua, Mexico 45:615-676
  Utah, variation 2:16-28
Snowberry, longleaf
  Big sagebrush associations
    Northeastern Nevada 47:117-131
Soda Lake, Nevada, limnology 31:106-108
Soils
  Compaction after logging
    Northeastern California 48:117-120
  Desert, microorganisms 37:81-86
  Frost and infiltration rate, dunes and interspace
    Southeastern Nevada 50:41-46
  Nitrification, inhibition by acetylene 46:316-320
  Southeastern Idaho wildlands 44:265-271
  Texture and grassland species diversity
    Eastern Great Basin 33:163-168
Solanum dulcamara
  Naturalization, habitat, Central Utah 44:317-323
Soliperla
  sierra 43:30-44
  tillamook 43:30-44
Solpugids
  National Reactor Testing Station, Idaho 31:164-168
Sonoran Desert
  Shrubs, reptile population changes 41:129-138
Sorex
  monticolus
    Microhabitat use patterns in summer 50:387-389
  nanus, ecology and habitat 50:161-165
  preblei, distribution, Northern Great Basin 50:93-95
South Dakota
  Badgers, winter stomach contents 43:492-493
  Black Hills
    Ponderosa pine overstory and forage quality 48:78-82
  Conata Basin, Burrowing Owl foods 45:287-290
South Dakota, Eastern
  Gray Partridge foraging ecology 48:202-205
South Dakota, Southwestern
  Black-tailed prairie dogs
    Rodenticide-treated site reoccupation 47:339-343
South Dakota, Western
  Black-tailed prairie dogs
    Ecology, associated species 50:339-345
  Prairie dog rodenticide
    Effects on deer mice 50:347-353
  Swift foxes, denning habitat and diet 46:249-253
Southwestern Research Station
  American Museum of Natural History 14:91
Spaniacris
  Bioecology, Colorado Desert, California 35:113-120
Spanworm, walnut
  Bionomics and control on bitterbrush, Utah 41:290-297
Spea, systematics 49:503-510
Spermatophthorus ***aberrans*** 28:1-15
Spermophilus
  beecheyi
    Agonistic behavior 48:19-24
    Burrow location 35:402-404
  beldingi beldingi
    Body size, organ size and sex ratios 35:305-309
    Reproductive cycle 35:427-433
  columbianus
    Seasonal activity, Idaho Primitive Area 40:175-177
  columbianus columbianus
    Cranial measurements 44:505-508
  elegans
    Helminth parasites 47:103-104
    Time budgets 41:221-228
  richardsonii
    Ecology, Laramie Basin, Wyoming 30:55-70
  townsendii
    Food, Arid Land Ecology Reserve, Washington 37:128
    Size and overlap of home ranges 49:108-110
Sphaeralcea
  grossulariifolia ***moorei*** 40:27-37
  leptophylla ***janeae*** 40:27-37
  psoraloides 40:27-37
Sphaerotrypes
  bengalensis 48:31-38
  costatus 48:31-38
  cristatus 48:31-38
  pentacme 48:31-38
  ranasinghei 48:31-38
Spherical densiometer
  Estimation of canopy cover 48:224-227
Sphodrocepheus ***anthelionus*** 28:176-178
Spiders
  Blackwidow, male bite, Utah 34:82
  Cache County, Utah
    Size, seasonal activity 44:104-110
  Collected from wild sunflowers
    Southwestern United States 47:280-282
  Grass, Organ Pipe Cactus National Monument, Arizona 45:546-547
  National Reactor Testing Station, Idaho 29:105-108
  Nevada Test Site 27:11-25
  Unusual population in Utah 33:51-52
  Utah, checklist, distribution 43:494-522
  Wolf, bite of 38:478
Spinibdella ***mali*** 27:98-101
Spinolidia
  magna 48:232-249
  sarmenta 48:232-249
Spittlebugs, cone
  Bionomics on mugo pine, Idaho 44:338-348
Splendidofilaria
  columbensis 36:445-457
  hibleri 36:445-457

- Sponges
  - Fossil, Garden City Limestone, Idaho 37:475-480
  - Lithistid, Devonian specimens in Nevada 36:206-210
- Spotted fever
  - Wood ticks, Utah recreational sites 33:26-28
- Springfish
  - Railroad Valley
    - Response to temperature 40:359-360
  - White River
    - Foods and feeding periodicity 49:249-251
- Spruce
  - Dwarf mistletoe effects
    - White Mountains, Arizona 46:685-689
  - Dwarf mistletoe infection
    - Southwestern United States 46:528-534
  - Engelmann, cone losses, insects
    - Northern Utah 48:508-511
- Squawfish
  - Colorado
    - Life strategies 46:656-661
    - Spawning, Yampa River, Utah 45:127-140
  - Colorado River
    - *Ophiotaenia* parasites 41:445-448
- Squirrels
  - Abert's
    - Dorsal hair length and coat color 42:597-598
    - Effects of logging on, Utah 47:252-258
    - Post-Pleistocene dispersal, modern distribution 49:425-434
  - Beechey ground, burrow location 35:402-404
  - Belding ground
    - Body size, organ size, and sex ratios 35:305-309
    - Juvenile, body size, composition, behavior 34:121-134
    - Reproductive cycle 35:427-433
  - California ground, agonistic behavior 48:19-24
  - Columbian ground
    - Juvenile, development and ecology 40:362-364
    - Seasonal activity, Idaho Primitive Area 40:175-177
  - Ground, cranial measurements 44:505-508
  - Interactions with mycorrhizal fungi
    - Oregon coniferous forests 48:358-369
  - Richardson's ground
    - Ecology, Laramie Basin, Wyoming 30:55-70
  - Thirteen-lined ground
    - Spatial and behavioral features 41:243-246
  - Townsend ground
    - Food, Arid Land Ecology Reserve, Washington 37:128
    - Size and overlap of home ranges 49:108-110
  - Uinta ground
    - Body fat, water and total caloric value 44:176-177
    - Holocene predation by badger 50:385
  - White-tailed antelope
    - North Central Nevada 44:428-430
  - Wyoming ground
    - Helminth parasites 47:103-104
    - Time budgets 41:221-228
- *Stagnicola pilsbryi* 31:223-236
- *Stalolidia* ***crista*** 49:398-403
- *Stanleya pinnata gibberosa*
  - Systematics, Wyoming 43:684-686
- Stansbury Mountains, Utah, flora, checklist 43:619-646
- Starling, breeding range expansion, Utah 35:419-424
- ***Stegomerus*** (Coleoptera) 27:119-141
  - ***chiriquensis*** 27:119-141
  - ***mexicanus*** 27:119-141
  - ***montanus*** 27:119-141
  - ***pygamaeus*** 27:119-141
  - ***vulgaris*** 27:119-141
- *Stenamma* ***knowltoni*** 32:35-39
- *Steniolia elegans*, nesting behavior of 33:29-30
- *Stenistomera*, systematics 39:351-418
- *Stenogonum*, systematics 36:272-280
- ***Stenolidia magna*** 46:134-136
- *Stenopelmatus*
  - ***cahuilaensis*** 28:124-131
  - ***mescaleroensis*** 39:226-230
- *Stephanitis*
  - ***charieis*** 21:108-113
  - ***kardia*** 20:29-38
- *Stephanomeria tenuifolia* ***uintaensis*** 43:375
- *Sternotherus*, systematics, North America 34:42-44
- ***Stictylus*** (Nematoda) 2:37-85
  - ***asymmetricus*** 2:37-85
  - ***obtusus*** 2:37-85
- *Stizostedion vitreum*
  - Green River Basin, Colorado and Utah 50:33-40
- Stoneflies
  - Distribution
    - Nevada and Utah 39:289-292
    - New Mexico 43:585-591
  - Nearctic, as ecological indicators 39:241-244
  - Nymph growth, constant high temperatures 35:51-61
- Storey, Margaret Hamilton 20:59-69
- ***Stragulotingis*** (Coleoptera) 29:129-132
- Strawberry Valley, Utah
  - Differential effects, cattle, sheep grazing 45:141-149
- Stream ecology, Huntington River, Utah 44:231-256
- *Sturnis vulgaris*
  - Breeding range expansion, Utah 35:419-424
- ***Stylolidia*** (Homoptera) 46:137-139
  - ***cristata*** 46:137-139
  - ***pectinata*** 46:137-139
- Substrate color matching, *Circotettix rabula* 34:60-70
- Succession
  - *Cupressus arizonica* 40:254-264
  - Following wildfire, pinyon-juniper woodlands
    - Great Basin 45:556-566
  - Lodgepole pine
    - Southern Rocky Mountains 43:447-455
  - Pinyon-juniper woodlands
    - Foliage biomass and cover 50:121-134
  - Spruce-fir forest zone, Northern Utah 40:1-26
  - Trembling aspen
    - Southern Rocky Mountains 43:447-455
- Suckers

- Coexistence of two species
  - Sagehen Creek, California 49:540-551
- Flannelmouth, growth and reproduction
  - Colorado River 45:281-286
- Longnose, parasitized by *Trichophrya*
  - Yellowstone Lake 45:255-265
- Parasites, Southern Utah 40:149-156
- Razorback
  - Early development 42:553-561
  - Ecology, Lower Colorado River 49:71-78
- Tahoe, reproductive ecology
  - Pyramid Lake, Nevada 38:181-186

Suctobelba ***tumulata*** 36:496-500

Supersaurus vivianae 45:697-709

Survey techniques, carnivores, small 43:438-440

Swallow bugs, American
- Barn and Cliff Swallow nest occupants, Colorado 47:345-346

Swallows, albino, Utah 17:29

Sweltsa ***gaufini*** 33:91-108

Sylvan Springs, Yellowstone National Park
- Shore bugs and flies, distribution 44:99-103

Sylvilagus
- *floridanus*
  - Introduced population, dispersal 41:167-175
- *idahoensis*
  - Oregon, habitat and distribution 44:563-571

Symbos cavifrons
- Delta County, Colorado 45:455-461
- Pleistocene, Southeastern Idaho 47:239-251

Symphoricarpos oreophilus
- *Artemisia tridentata vaseyana* associations
  - Northeastern Nevada 47:117-131

Synechococcus lividus
- Effect of elevated temperature on copper toxicity 41:255-258

Synhalonia fulvitarsis
- *Phlox bryoides* visitation 39:197-198

Syntormon ***californicum*** 11:11-17

Syzygioxylon ***chhindwarense*** 37:241-246

T

Tachysphex, nesting, predatory behavior
- Western United States 45:293-298

Taenia taeniaeformis
- Prevalence in *Microtus pennsylvanicus*, Montana 37:252

Talinum ***thompsonii*** 45:485-487

Tamarix ramosissima
- Habitat relationships, Central Utah 46:535-541

Tanner, Annie Atkin 30:190-194

Tanner, Vasco M. 30:181-189; 30:190-194; 30:195; 30:196; 30:197-199; 30:201-202; 30:203-204; 30:205-206; 30:207-208; 30:209-210; 30:211-212; 30:213-215; 30:216-217; 30:218

Tannerocoris sarcobati 30:227-231

Tantilla utahensis, distribution 22:116-118

Taphrodasus (Scolytidae) 40:89-97

Teniulus (Paraiulidae) 11:19-26
- ***parvior*** 11:19-26
- ***setosior*** 11:19-26

Tertiary
- Fossil palm, Dipping Vat Formation, Central Utah 32:1-15

Tesserocerus ***forceps*** 26:45-70

Teton Range, Wyoming
- Alpine vascular plants, checklist 41:232-242

Texas, *Hydroperla crosbyi*, life cycle 37:260-273

Thada (Nematoda) 2:37-85
- ***cancellata*** 2:37-85
- ***striata*** 2:37-85

Thagria
- ***bifida*** 46:321-328
- ***insolentis*** 46:321-328
- ***marissae*** 46:321-328
- ***melichari*** 46:321-328
- ***unidentata*** 46:321-328

Thamnophis
- *elegans* ***arizonae*** 49:511-516
- *elegans* ***vascotanneri*** 49:511-516
- *ordinoides vagrans*
  - Number, length, and weight of the young 9:51-54
- *rufipunctatus* ***unilabialis*** 45:615-676
- *sirtalis* ***lowei*** 48:499-507

Thamnophothorus ***impensus*** 21:1-7

Thaumastoptera ***hynesi*** 24:19-25

Thelesperma
- ***pubescens*** 43:749-750
- *subnudum* ***alpinum*** 43:369-370

Thelypodiopsis ***argillacea*** 37:95-96

Thelypodium sagittatum ***vermicularis*** 37:279-365

Thiabendazole
- Efficacy as sheep anthelmintic 29:35-41

Thinning, lodgepole pine
- Vegetation and big game effects 42:512-516

Thioploca ingrica, Zion National Park, Utah 40:98-100

Thomomys
- *bottae*
  - Hybridization with *townsendii*, California 44:431-440
- *talpoides*
  - Albinism in Colorado 31:181
  - Spruce-fir forests 41:362-367
- *townsendii*
  - Hybridization with *bottae*, California 44:431-440

Thysanoes
- ***berbericolens*** 31:69-76
- ***tuberculatus*** 35:21-32

Ticks
- Oviposition and egg development 17:42-51
- Rocky Mountain wood
  - National forest sites, Utah 28:30-43
- Wood, spotted fever in, Utah recreational sites 33:26-28

Time budgets, *Spermophilus elegans* 41:221-228

Timpie Springs, Utah, aquatic macrobiota 42:77-80
Tingis
  agrana 24:27-30
  bengalana 16:18-22
Tinocripus ***huggerti*** 48:232-249
Tintic Mountains, Utah
  Cryptogamic soil crusts, seasonal algal variation 45:14-21
Tipula
  carsoni 23:159-165
  chumash 21:10-16
  cladacanthodes 24:19-25
  denali 29:1-10
  denningi 29:1-10
  dis 22:1-7
  epios 29:1-10
  estella 30:232-241
  eurystyla 29:1-10
  flinti 30:232-241
  footeana 21:10-16
  frommeri 33:189-196
  gertschi 23:159-165
  grahamina 23:159-165
  hastingsae ***diperona*** 33:189-196
  hedgesi 21:10-16
  horningi 26:1-8
  incisa ***picturata*** 21:79-86
  kirkwoodi 21:79-86
  knowltoniana 29:1-10
  linsdalei ***obispoensis*** 22:1-7
  macleani 33:189-196
  mckinleyana 29:1-10
  mecotrichia 26:1-8
  mercedensis 25:49-53
  metacomet 25:49-53
  paterifera 22:1-7
  perhirtipes 23:159-165
  productisterna 23:159-165
  sacra 5:93-103
  sanctaecruzae 33:189-196
  saylori 21:79-86
  simondsi 25:49-53
  smithae 28:16-23
  toklatensis 28:16-23
  triplex ***integra*** 22:1-7
Toads
  Arizona-Sonoran Desert
    Sexual selection and mating 45:688-696
  Boreal, breeding behavior
    Western Montana 31:109-113
  Colorado River, type specimen 28:70-72
  Great Basin spadefoot, Utah 45:22-30
  Hybrid between Great Plains and red-spotted
    Central Arizona 50:371-372
Tomato, Ace 55, cold acclimation 40:121-126
Topminnows, Sonoran
  Management, Bylas Springs, Arizona 50:265-273
Torenia asiatica
  Chemical effects on pollen germination 34:71-81
Tortoise, desert
  Courtship behavior 36:467-470
  Plasma protein marker for population genetic studies 50:1-8
Townsendia
  jonesii ***lutea*** 43:369-370
  montana ***caelilinensis*** 43:369-370
  Systematics, keys, Utah 30:23-52
Tradescantia
  Effects of uranium mill tailings on 38:456-462
Transferrin polymorphism
  Bighorn sheep, Colorado 40:141-142
Trapping methods, insects, rangeland 48:383-387
Trepobates ***panamensis*** 12:35-38
Trichopetalum ***montis*** 11:19-26
Trichophrya, Yellowstone Lake
  Infesting brook trout, longnose suckers 45:255-265
Trichoptera
  Biology 40:287-291
  Southeastern Idaho, checklist 37:253-257
  Species, emergence, habitat
    Sagehen Creek Basin, California 49:186-197
Tricolus
  saundersi 27:119-141
  spectibilis 27:119-141
Trifolium andersonii ***friscanum*** 38:225-367
Trimerotropis
  agrestis ***barnumi*** 20:49-58
  agrestis ***gracewileyae*** 20:49-58
  agrestis ***hewitti*** 24:31-35
  citrina ***neomexicana*** 21:51-54
Triodopsis cragini, type locality 14:87-89
Trischidias ***exigua*** 46:265-273
Triticeae, systematics, keys
  Intermountain Region 43:561-572
Triznaka ***spinosa*** 41:349-359
Trombicula
  allredi 15:1-26
  doremi 15:1-26
  lacerticola 24:13-17
  reesi 17:95-102
Trout
  Attack by clam 14:23-25
  Brook
    Effects of watershed alteration 46:39-45
  Brown
    Internal parasites, Montana 35:442-448
    Water fertility and reproduction, Montana 35:435-441
  Cutthroat
    Electrophoretic study, Utah 45:677-687
    Food size selection, Palisades Creek, Idaho 45:327-331
    Parasitized by *Trichophrya*, Yellowstone Lake, Wyoming 45:255-265
    Western Bonneville Basin, subspecies status 38:193-202

    Yellowstone Park, *Diphyllobothrium cordiceps* larvae in 44:125-133
  Lahontan cutthroat
    Life history in Pyramid Lake, Nevada 43:1-29
    Spawning behavior variability, Nevada 47:480-487
Trypophloeus populi
  Bionomics 37:105-127
  Emergence data, artificial rearing media 39:129-132
Tularemia
  Deer fly vectors, Utah Lake, Utah 25:13-29
  Utah and the Great Basin 39:103-121
Tundra vegetation
  San Juan Mountains, Colorado 45:87-93
Turkeys
  Merriam's Wild
    Habitat and home range, Oregon 49:252-258
  Postglacial, Northern Great Basin 31:48-49
Turtles
  Fossil, Green River Formation, Utah 30:13-15
  North American musk, generic name 34:42-44
  Systematics, Western Chihuahua, Mexico 47:383-421
Tympanuchus pallidicinctus
  Nest site selection and vegetation characteristics, Texas 49:624-626
Typha latifolia, decline, Farmington Bay, Utah 37:24-34
Typhlodromus mcgregori
  Control of mites in apple orchards 37:366-374
Typhlodromus occidentalis
  Reproduction and prey type available 32:61-75
Typhlops
  adamsi 11:53-86
  becki 9:1-20
Tyto alba, sexual imprinting on humans 36:385-386

U

Uinta Basin, Utah
  Birds 18:23-25
  Eriogonum corymbosum, ecology 39:177-191
  Spring waterfowl migration 37:274-278
  Vegetation and soil factors 42:81-90
Uinta Mountains, Utah
  Invertebrate fauna, caves, checklist 41:207-212
  Wetland plant communities 43:523-530
Uinta National Forest, Utah
  Raptors 38:438-446
Uintah Basin, Utah
  Soil algae of cryptogamic crusts 45:432-442
Uintah County, Utah
  Birds, checklist, distribution 44:584-620
Ulmus pumila, Utah, naturalization 24:103-106
Ultrasaurus macintoshi 45:697-709
Umbelliferae, *Oreoxis*, systematics, Utah 45:34-36
Understory vegetation
  Environmental and vegetational parameters 40:167-174
  Pinyon-juniper stands, Nevada 41:467-475
  Response to pinyon-juniper harvesting
    Great Basin 45:105-112
United States
  Earthworms, deserts 27:142-176
United States, Southwestern
  Boraginaceae, systematics, keys 39:293-350
  Coal mine spoils, reclamation 44:441-446
  Dwarf mistletoe
    Infection of young Douglas-fir 50:67-71
  Floristic analysis 46:46-65
  Local floras, bibliography 42:105-112
  Ponderosa pine site potential estimation 47:467-472
  Spider fauna on wild sunflowers 47:280-282
United States, Western
  Land survey notes, used to reconstruct presettlement landscapes 50:181-191
  Mammals, plague important 12:67-75
Universal soil loss equation
  Applicability, Southeastern Idaho 43:579-584
Uranium mill tailings
  Effects of radiation on *Tradescantia* 38:456-462
Uroblaniulus
  dixinus 11:19-26
  exul 11:19-26
Urosaurus, phylogenetic relationship to *Uta* 35:245-268
Ursus americanus, Carson Range, Nevada
  Co-occupancy of a den 49:390-391
Uta
  Phylogenetic relationship to *Urosaurus* 35:245-268
  stansburiana
    Systematics, Utah 30:71-90
  stansburiana stansburiana
    Reproduction, Southwestern Idaho 43:477-482
  stansburiana stejnegeri
    Ecology, Dona Ana County, New Mexico 33:124-128
  stansburiana ***uniformis*** 30:71-90
Utabaenetes tanneri 30:242-249
Utah
  Abert squirrels, effects of logging on 47:252-258
  Algae, checklist 48:154-179
  Antelope Island, Great Salt Lake
    Barn Owl diet and mammals 46:307-309
  Ants, systematics, keys, distribution 42:415-511
  Apple maggot, adaptation for cherries 46:173-174
  Apple orchards, phytoseiid pest predators 39:63-80
  Aquatic biology, bibliography 22:32-53
  Barn Owls, seasonal food habits 32:229-234
  Bear River marshes
    Unusual winter visitors or late migrants 3:51-53
  Birds 33:243-245
    Breeding records 3:61-85
    Distribution and breeding 43:717-727
  Bombylius, systematics, keys 35:407-418
  Bonneville Basin
    Pocket mice reproduction 50:361-365
  Bristlecone pine ecology 44:487-494
  Bryce Canyon Breaks, vegetation 43:701-712

Bryce Canyon National Park
  Drosophila pseudoobscura, experimental release 47:32-37
  Vascular flora, checklist 48:352
Cache County
  Spiders, size, seasonal activity 44:104-110
Cactaceae, systematics, keys 44:52-69
Camp Floyd State Park
  Cryptogamic soil crusts 46:632-640
Canids, late Pleistocene 46:415-420
Canyon Mountains
  Vascular plant checklist 44:277-295
Canyonlands National Park
  Ecological distribution of rodents 39:199-205
Capitol Reef National Park
  Utah prairie dog reestablishment 42:517-523
Castle Cliffs
  Vegetation patterns 45:535-541
Chenopodiaceae, systematics, keys 44:183-209
Chiggers, checklist, keys 15:1-26
Chokecherry, black knot disease 44:579-583
Church Mountains
  Vascular plant checklist 44:277-295
Collembola 13:43-46
  Checklist 16:7-8
Colorado River system
  Peregrine Falcon nesting habitat 49:408-418
Compositae, systematics, keys 43:179-357
Cone rust on *Picea pungens* 42:262-272
Conifer distribution 31:177-180
Corrine, Pleistocene *Gila atraria* 49:131-133
Coyotes, food habits on deer herds 43:432-437
Crayfish, distribution 46:625-631
Crystal Ball Cave
  Quaternary paleontology and paleoecology 45:337-390
Curlew Valley
  Desert shrub phytomass and minerals 44:327-337
  Raptors, nesting 31:51-65
Cutthroat trout, electrophoretic study 45:677-687
Deer Creek Reservoir
  Yellow perch, parasites 31:169-176
Deer hunter responses to checking station questionnaire 49:159-166
Dermacentor andersoni
  National forest sites 28:30-43
Diplostomum spathaceum, life cycle 36:86-96
Dixie State Park
  Dipodomys merriami, burrowing habits 31:190-192
Duchesne County, algal populations in Bottle Hollow Reservoir 42:205-218
Dugway, mites 13:35-42
Dytiscidae, keys, distribution 22:54-75
Elk and mule deer diet similarity 49:552-555
Eumeces skiltonianus skiltonianus
  Life history 4:81-88
Farmington Bay, *Typha latifolia* decline 37:24-34
Fish hatchery history 46:583-594
Fish Springs, Mollusca 31:223-236
Flaming Gorge Reservoir
  Kokanee reproductive characteristics 48:46-50
Flea-host associations 12:67-75
Fleas, host and distributional records 26:71-75
Flora
  Desert and mountain comparative studies 43:385-393
  Miscellaneous families, systematics, keys 40:38-58
Gentianaceae, systematics, keys 36:483-495
Geranium, systematics, keys 34:297-304
Goshen Ponds, diatom flora 38:211-214
Goshen, Utah County, salt playa vegetation 39:44-58
Great Basin pocket mouse, distribution 18:26-30
Great Basin spadefoot toad 45:22-30
Great Salt Lake
  Biological investigations, summary 34:221-229
  California Gull nesting populations 50:299-302
  Insular biogeography of mammals 42:589-596
  Nesting waterfowl response to wetland flooding 49:614-617
  Water for lobster culture 39:231-240
Great Salt Lake Desert, sucking lice, keys 16:9-17
Great Salt Lake Islands, birds, checklist 37:247-251
Green River Formation, fossil turtle 30:13-15
Hanging gardens, distribution, diversity 49:1-30
Helminths of *Sceloporus* lizards 33:1-18
Henry Mountains
  Wahweap milkvetch population cycles, seed reserves 48:541-547
House Range
  Vascular plant checklist, communities 48:102-116
Huntington River
  Ecology of a regulated stream 44:231-256
Hydrophyllaceae, systematics, keys 36:1-55
Juncaceae, systematics, keys 46:366-377
Juniper woodland decreases since settlement 39:263-266
Kaiparowits Region, biotic study 1:97-126
Kane County
  Ceratoides lanata, grazing pressure 46:148-156
Kings Peak, Uinta Mountains
  Alpine plant communities 42:50-59
Lily Lake
  Aquatic Phycomycetes 32:181-189
  Diatom floristics and succession 39:15-43
Logan Canyon
  Cliff chipmunk, food preferences 31:182-188
  Dendroctonus pseudotsugae broods on *Pseudotsuga menziesii* 48:348-351
Malvaceae, systematics, keys 40:27-37
Mammals
  Bibliography, checklist 2:125-136
  Distributional patterns 37:457-474
Marsh plants
  Comparison of burning and cutting 45:462-466
Melanoplus, distribution, economics 5:1-22
Mill Creek, Wasatch Mountains

  Megarcys signata, life history and ecology 35:39-48
Mites
  Parasitizing *Peromyscus* 16:23-31; 17:95-102
  Unusual records 26:34
Mottled sculpin 47:13-21
Mountain brush vegetation
  Comparative study 27:59-66
Mount Timpanogos
  Ambystoma tigrinum nebulosum, life history 31:213-222
  Aphids, checklist 7:1-6
Mule deer
  Changes in size 49:31-35
  Gender-related mortality 44:450-452
  Maxillary canine teeth 43:445-446
  Predator control 37:101-102
Nesting habits, mountain-dwelling birds 2:1-8
Nighthawk distribution 1:93-96
Oakbrush compositional similarity 41:147-153
Oil Shale Tracts
  Wildlife distribution, abundance 46:469-507
Omophronidae, keys 2:99-104
Orange Cliffs, flora, checklist 47:287-298
Paunsagunt Plateau Region, mammals 26:43-44
Phalacrocorax auritus auritus, breeding 37:1-23
Plants
  Names, author index 42:385-394
  Poisonous, checklist 40:229-253
  Rare 45:173-236
  Types, list, historical perspective 42:129-195
Pleistocene Trumpeter Swan 46:547-548
Polygonaceae, systematics, keys 44:519-557
Predaceous-scavenger ants 27:67-78
Provo River, macroinvertebrates, checklist 32:211-219
Raft River Mountains
  Seed, cone insects with *Pinus monophylla* 44:349-356
  White locoweed, soil-site relationships 49:419-424
Revegetation of gopher mounds 34:267-275
Ring-necked Pheasants
  Nest-site selection 41:457-460
  Overwinter survival 41:247-250
Robber flies, systematics, keys 47:38-90
Rock Island, Utah Lake, water birds 6:127-128
Rocky Mountain streams
  Macroinvertebrate colonization 45:117-123
Rosaceae, systematics, keys 42:1-44
Rush Valley
  Rodent populations in *Artemisia tridentata* 35:191-202
Sagebrush wilt disease 41:184-191
Salicaceae, systematics, keys 43:531-550
San Rafael Swell, vascular flora, checklist 43:79-87
Sanpete County
  Dog owners and hydatid disease knowledge 40:216-220
Saxifragaceae, systematics, keys 45:155-172
Scorpions 32:154-170
Sheeprock Mountains
  Blue Grouse winter habitats and foods 49:229-232
Siberian elm naturalization 24:103-106
Silver Creek, Pleistocene vertebrates 36:387-424
Simuliidae, keys and distribution 20:81-104
Siphonaptera, distribution 10:62-65; 11:105-114
Snakes, variation 2:16-28
Southern Wasatch and Uinta Mountains
  Biotic communities 6:1-124
Spiders
  Checklist, distribution 43:494-522
  Unusual population 33:51-52
Spotted fever in recreational sites 33:26-28
Stansbury Mountains, flora, checklist 43:619-646
Starling, breeding range expansion 35:419-424
Stoneflies, checklist 33:91-108
Timpie Springs, aquatic macrobiota 42:77-80
Tintic Mountains
  Cryptogamic soil crusts, seasonal algal variation 45:14-21
Townsendia, keys, distribution 30:23-52
Tularemia 39:103-121
Uinta Basin
  Birds 18:23-25
  Eriogonum corymbosum, ecology 39:177-191
  Spring waterfowl migration 37:274-278
  Vegetation and soil factors 42:81-90
Uinta Mountains
  Wetland plant communities 43:523-530
Uinta National Forest, raptors 38:438-446
Uintah Basin
  Soil algae of cryptogamic crusts 45:432-442
Uintah County
  Birds, checklist, distribution 44:584-620
Utah County
  Parasites of Indochinese refugees 41:201-206
Utah Lake
  Algae, checklist 30:99-105; 31:125-134; 45:237-254
  California Gulls, banding 2:98; 3:55-57; 8:37-39
  California Gulls, life history 3:91-108
  Carp and white bass diel behavior 44:509-515
  Environmental interaction in algal communities 38:31-41
  Phytoplankton distribution 39:245-252
  Plant community zonation in saline meadow 47:322-333
  Tularemia and deer flies 25:13-29
  White bass, spawning ecology 28:63-69
Utah Valley, helminth parasites 30:131-145
Vascular plants
  Checklist 41:1-108
  Systematics 46:254-260; 46:261-264
Vegetation, bibliography 50:209-242
Vireo gilvus swainsonii occurrence 29:181-182
Virgin River, endemic fish parasites 46:662-676
Wallsburg, impact of 1975 fire on antelope bitterbrush 40:299-302

Walnut spanworm
  Bionomics, control on bitterbrush 41:290-297
Wasatch Mountains
  Salamander mass mortality by *Acinetobacter* 49:364-372
  Reproduction of subalpine herbs 43:573-578
Washington County
  Elevational changes in woody vegetation 48:512-529
  Spotted bats, roosting behavior 35:121-122
Western Meadowlark, insect food 4:101-102
White River, Uintah County, aquatic birds 45:113-116
White-tailed prairie dogs
  Diggings in western harvester ant mounds 49:36-37
Yampa River
  Colorado squawfish, spawning 45:127-140
Yellow-headed Blackbirds, territories 1:75-91
Zion National Park
  Hanging gardens, dispersal types, flood frequency 40:365-371
  Hanging gardens, the Narrows 40:178-182
  Physa zionis, distribution 46:310-315
  Thioploca ingrica on wet walls 40:98-100
Zygoptera, distribution and biology 35:379-390
Utah, Central
  Atriplex confertifolia, community ecology 46:348-357
  C3 and C4 plant species
    Ecological differences 46:140-147
  Cestode infections in sheep dogs 46:208-216
  Cliffrose
    Stem circumference, diameter and age 47:334-338
  Cowania mexicana stansburiana, ecology 47:132-151
  Ducks, time-activity budgets 48:280-284
  Echinococcus granulosus
    Prevalence in sheep dogs 42:65-66
  Elaeophora schneideri, prevalence 42:351-352
  Glaux maritima, habitat relationships 44:299-309
  Grazing impacts, sagebrush communities 41:335-340
  Growth variation, white and Douglas-fir 39:219-225
  Helminth parasites of cats and dogs 36:471-474
  Hydatid disease, control 43:65-72
  Onchocerca cervipedis, prevalence 42:351-352
  Phytoseiid mites
    Overwintering in apple orchards 29:96-104
  Ring-necked Pheasants
    Winter behavior, habitat 42:562-566
  Saltcedar habitat relationships 46:535-541
  Sarcobatus vermiculatus
    Community ecology 46:348-357
  Screech Owls, winter food 31:83-84
  Solanum dulcamara
    Naturalization, habitat 44:317-323
  Strawberry Valley
    Beaver foraging in aspens 48:250-262
    Differential effects of cattle, sheep grazing 45:141-149
  Swainson's Hawks, feeding and behavior 46:302-304
  Tertiary Dipping Vat Formation, fossil palm 32:1-15
  White-lined sphinx moth, abundant 1940 9:76
Utah, Northeastern
  Birds, Uinta Mountains and Basin 18:1-22
  Diatoms 44:36-48
  Invertebrates, caves, Uinta Mountains 41:207-212
Utah, Northern
  Aphytis vandenboschi
    San Jose scale parasite 48:388-393
  Black-tailed jackrabbits
    Home range and activity patterns 50:249-256
  Engelmann spruce cone losses by insects 48:508-511
  Insect communities and faunas 45:37-60
  Relict stands of pinyon hybrids 32:171-175
  Spruce-fir zone succession 40:1-26
  Studies of the San Jose scale parasite
    Aphytis vandenboschi 48:388-393
Utah, Southeastern
  Late Quaternary, plant zonation and climate 44:1-35
  Plant chemical composition and mule deer reproduction 39:122-128
Utah, Southern
  Ant ecology 39:97-102
  Desert rodent population
    Habitat manipulations 49:435-448
  Fire history, Paunsaugunt Plateau 48:58-63
Utah, Southwestern
  Barrel cactus
    Orientation and slope preference 44:133-139
  Blackbrush community
    Habitat relationships 45:321-326
  Spotted bat, notes 34:254-256
Utah, West Central
  Ferruginous Hawks, ground nesting 28:111
  Reproduction in three sympatric lizards 40:68-72
Utah, Western
  Cliff chipmunk, genetic variation 47:551-561
  Ermine 28:47
  Flea exchange, deer mice and rodents 36:475-480
  Raptor mortality 29:165-167
Utah County, Utah
  Parasites of Indochinese refugees 41:201-206
Utah Lake, Utah
  Algae, checklist 30:99-105; 31:125-134; 45:237-254
  California Gulls
    Banding 2:98; 3:55-57; 8:37-39
    Life history 3:91-108
  Carp and white bass diel behavior 44:509-515
  Environmental interaction
    Algal communities 38:31-41
  Phytoplankton distribution 39:245-252
  Plant community zonation
    Saline meadow 47:322-333
  Tularemia and deer flies 25:13-29
  White bass, spawning ecology 28:63-69
Utah Museum of Natural History
  Mammal type specimens 47:620-624
Utah Valley, Utah, helminth parasites 30:131-145

Utamias dorsalis
  Food preferences, Logan Canyon, Utah 31:182-188
Utamphorophora timpanogos 7:1-6

V

Van Dyke, Edwin Cooper 13:29-34
Vanclevea, anatomy and taxonomy 34:151-160
Vegetation
  Alpine, Schoolroom Glacier, Wyoming 43:483-491
  Annual and perennial, spatial and temporal variability
    Chaco Canyon, New Mexico 49:113-122
  Avalanche response
    Glacier National Park, Montana 45:313-317
  Bibliography, Nevada and Utah 50:209-242
  Bryce Canyon Breaks, Utah 43:701-712
  Colorado
    Bibliography 43:45-64; 44:677-680
    Preliminary classification 44:647-676
  Frequency values and summation, Idaho 47:299-307
  Mima mounds, Kalsow Prairie, Iowa 42:246-261
  Montana, bibliography 48:301-323
  Mountain meadow
    Frequency sampling, quadrat and sample size
      49:241-248
  Patterns
    Avalanche paths, Northern Rockies, Montana
      44:453-458
    Bulldozing and chaining, Utah pinyon-juniper
      46:508-512
    Castle Cliffs, Utah 45:535-541
  Pine Butte Fen, Montana 46:22-32
  Postglacial
    Laramie Basin, Wyoming-Colorado 43:377-384
  Presettlement
    Moffat County, Colorado 45:747-777
    Piceance Basin, Colorado 43:687-699
  Response
    Moisture gradient, Central Arizona 39:161-176
    Retained mine highwall, South Central Wyoming
      49:449-455
  Riparian, classification
    Western Colorado 49:214-228
  Salt playa, Goshen, Utah 39:44-58
  Southwestern United States
    Floristic analysis 46:46-65
  Tundra, San Juan Mountains, Colorado 45:87-93
  Understory, pinyon-juniper, Nevada 41:467-475
  Woody, elevational changes
    Washington County, Utah 48:512-529
Vegetational attribute measurement, Idaho 47:299-307
Verdin, body composition
  Clark County, Nevada 31:66-68
Veromessor ***lariversi*** 11:91-96
Vertebrates
  Bighorn Canyon National Recreation Area
    Checklist, distribution 47:512-521
  Collections, contributed by Owen Bryant 9:47-49
  Communities, vegetation influence
    Great Basin 46:711-720
  Idaho National Environmental Research Park
    46:513-527
  Kaiparowits Basin, checklist, distribution 40:303-350
  Pleistocene
    Systematics, Silver Creek, Utah 36:387-424
  Response to retained mine highwall
    South Central Wyoming 49:449-455
  Southeastern Idaho
    Radioactive leaching pond 38:64-70
  Terrestrial, Scotts Bluff National Monument
    Nebraska, checklist 49:597-613
  Utah oil shale tracts
    Distribution and abundance 46:469-507
Vireo gilvus swainsonii, occurrence in Utah 29:181-182
Virgin River
  Fish thermal tolerances 47:538-546
Virgin River, Utah
  Endemic fish parasites 46:662-676
Viscainopelmatus (Orthoptera) 30:173-179
  davewerneri 30:173-179
    Systematics 34:203-206
Voles
  Montane
    Hip glands 44:468-470
    Indomethacin wheat, population control 49:556-561
  Red-backed
    Microhabitat selection 48:216-223
    Mycophagy 48:269-273
    Short-term effects of logging on 40:183-189
  Sagebrush
    Burrows, Southeastern Idaho 47:276-279
Vulpes
  macrotis nevadensis, arthropod consortes 20:71-77
  velox
    Denning habitat and diet, South Dakota 46:249-253
Vultures, Turkey, roosting site decline
  Oregon 46:305-306

W

Walker Lake, Nevada
  Gila bicolor, reproduction and embryology 42:60-64
  Tui chub, biology 45:784-788
Wallsburg, Utah
  Impact of 1975 fire on antelope bitterbrush
    40:299-302
Walnut Canyon National Monument, Arizona
  Juniper mistletoe hosts 38:89
Warm water aquaculture
  Waste heat and water from power plants 44:75-82
Warner Basin, Oregon
  Conservation status of threatened fishes 50:243-248
Warner Mountains, California
  White fir invasion of big sagebrush 35:319-324
Wasatch Mountains, Utah
  Reproduction of subalpine herbs 43:573-578

  Salamander mass mortality by *Acinetobacter* 49:364-372
Washington
  Arid Land Ecology Reserve

    Spermophilus townsendi, food 37:128
  Bobcat, autumn, winter food habits 44:70-74
Washington, Central
  Rodent botfly
    Field behavior and seasonal activity 34:247-253
Washington, Eastern
  Ambystoma tigrinum melanostictum, feeding habits 46:299-301
Washington, Southeastern
  Kramer Palouse Natural Area 43:421-424
Washington County, Utah
  Elevational changes in woody vegetation 48:512-529
  Spotted bats, roosting behavior 35:121-122
Wasps
  Brachycistidine
    Nevada Test Site, checklist 33:109-112
  Jackson Hole, Wyoming
    Checklist and ecology 33:147-155
  Mutillid, Nevada Test Site 33:156-162
Water
  Impoundment use by waterfowl and shorebirds
    Northern Great Plains 48:353-357
    Reduction from soil following prescribed burning 44:558-562
Water-striders
  Systematics
    Neotropical Region 11:37-42
    Venezuela 12:47-54
Waterfowl
  Nesting, response to flooding of wetlands
    Great Salt Lake 49:614-617
  Spring migration, Uinta Basin, Utah 37:274-278
Watershed alteration, effects on brook trout 46:39-45
Weevils
  Female genitalia and spermathecae 20:1-22
  Systematics, Western United States 10:71-73; 14:73-78; 19:53-55
West Elk Mountains, Colorado
  Alpine vascular flora, checklist 47:152-160
Whales, bowhead, parasites 47:355-372
White Mountains, Arizona
  Vegetation zones around a small pond 32:91-96
White River, Utah, aquatic birds 45:113-116
Wildrye, Great Basin
  Herbivorous and parasitic insects, Southern Idaho 47:644-651
Wilt disease, sagebrush, Utah 41:184-191
Winterfat
  Grazing pressure, Kane County, Utah 46:148-156
Woodbury, Angus Munn 25:81-88
Woodrats, genetic variation, Great Basin 46:577-580
Wormsnake, cape
  Baja California, correct name 34:94-96
Woundfin
  Biology, Virgin River Basin 38:463-468
  Parasites, Virgin River, Utah 46:662-676
  Spawning and growth 42:549-552
Wrens
  Rock, insect food 3:22
  House, bat boxes, utilization 43:456
Wyoming
  American White Pelican, nesting colonies 48:285-289
  California Gulls, nesting colonies 46:128-133
  Cavity-nesting birds, tree use 46:358-360
  Ciconiiforms
    Nesting, status and distribution 48:290-297
  Crayfish, checklist, management 48:370-372
  Eimeria species infecting Wyoming ground squirrels and white-tailed prairie dogs 50:327-331
  Exotic fishes 47:523-526
  Fossil Butte National Monument
    Mammals, preliminary survey 37:91-94
  Grand Teton National Park
    Bee visitors of sweetvetch 47:314-318
    Microtines, distribution and interspecies interaction 33:205-217
  Grand Teton National Park and vicinity
    Mosses, checklist 45:124-126
  Hutton Lake National Wildlife Refuge
    Prairie dog burrows 31:115-124
  Jackson Hole
    American marten demographics 49:587-596
    Philanthus, nests and prey 26:35-40
    Wasps, checklist and ecology 33:147-155
  Laramie Basin
    Floral resources on shortgrass prairie 40:197-215
    Richardson's ground squirrel, ecology 30:55-70
    Vegetation, postglacial 43:377-384
  Laramie Plains
    Thirteen-lined ground squirrels, behavior 41:243-246
  Little Box Elder Cave
    Late Pleistocene mammals 31:93-105
  Long-billed Curlew habitat comparisons 47:459-466
  Raccoons, distribution 42:599-600
  Recent Mollusca, checklist 49:637-645
  Schoolroom Glacier, alpine vegetation 43:483-491
  Snake River Canyon, Bald Eagles 41:461-464
  Teton Range
    Alpine vascular plants, checklist 41:232-242
  Yellowstone Lake, fish parasites 47:259-275
Wyoming, Central
  Coyote summer food habits 41:449-456
Wyoming, South Central
  Comparison of Sage and Sharp-tailed Grouse leks 49:275-278
  Wildlife response to retained mine highwall 49:449-455
Wyoming, Southeastern
  Arthropod effects in mountain shrub habitats, root:shoot ratio and biomass 49:456-460

Wyoming, Southwestern
  Breeding raptors
    Food habits, nest characteristics 48:548-553
  Winter habitat use by elk, moose, mule deer 47:538-643
Wyoming, Western
  Comandra umbellata, ecology 49:650-655

X

Xanthocephalus xanthocephalus
  Habitat and reproductive strategy 38:85-88
  Territories, Utah 1:75-91
Xenotingis
  luzonana 14:1-10
  papuana 14:1-10
Xerobates
  agassizi
    Plasma protein marker for population genetic studies 50:1-8
  lepidocephalus 49:496-502
Xyleborinus ***tribuloides*** 37:207-220
Xyleborus
  bicornatulus 27:119-141
  californicus 35:391-401
  devexus 37:207-220
  horridatus 27:119-141
  horridicus 27:119-141
  incultus 35:391-401
  laticeps 37:207-220
  longideclivis 28:1-15
  molestulus 35:391-401
  parcellus 28:1-15
  praestans 40:353-358
  tristiculus 35:391-401
  usticius 28:1-15
Xylechinosomus ***pilosus*** 45:266-275
Xylechinus
  ougeiniae 48:31-38
  padus 48:31-38
Xyrauchen texanus
  Early development 42:553-561
  Ecology, lower Colorado River 49:71-78

Y

Yampa River, Utah
  Colorado squawfish, spawning 45:127-140
Yellowstone Lake, Wyoming
  Parasites, cutthroat trout and longnose suckers 47:259-275
Yellowstone National Park
  Sylvan Springs shore bugs and flies, distribution 44:99-103
Yellowstone River, Montana
  Parasites of *Polyodon spathula* 35:425-426
Yucca
  harrimaniae ***sterilis*** 45:789-790
  toftiae 34:305-310

Z

Zapus princeps, home range, Colorado 37:87-90
Zelandotipula ***serratimargo*** 30:232-241
Zelanion ***hawaiiensis*** 13:75-85
Zenaida macroura
  Use of man-made ponds, Idaho 49:627-631
Zigadenus paniculatus
  Effects of defoliation on reproduction 42:524-528
  Reproductive biology 41:427-430
Zion National Park, Utah
  Hanging gardens
    Dispersal types, flood frequency 40:365-371
    Narrows region 40:178-182
  Physa zionis, distribution 46:310-315
  Thioploca ingrica on wet walls 40:98-100
Zooplankton orientation to oxycline
  Big Soda Lake, Nevada 49:535-539
Zygoptera, distribution and biology, Utah 35:379-390
Zygoribatula ***apletosa*** 35:103-108

2,4-D
  Long-term effects on *Populus tremuloides* 44:459-467

GREAT BASIN NATURALIST
MEMOIRS SERIES

The *Great Basin Naturalist Memoirs* series was established in 1976 for scholarly works in biological natural history of greater length than can be accommodated in the *Great Basin Naturalist*. The *Memoirs* series appears irregularly. Approval for the production is the responsibility of the *Great Basin Naturalist* Editorial Board. Information concerning the production of the *Memoirs* series can be obtained from James R. Barnes, Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, UT 84602.

GREAT BASIN NATURALIST MEMOIRS

All *Memoirs* are available for purchase. Direct inquiries to: Editorial Office, 290 MLBM, Brigham Young University, Provo, UT 84602. Only U.S. currency or checks or money orders drawn on U.S. banks are accepted. These should be made out to *Great Basin Naturalist*. Please include $3 per copy for mailing and handling charges except for Nos. 6 and 11. The charge for these volumes is $5 per copy.

No. 1 The birds of Utah. $15
No. 2 Intermountain biogeography: a symposium. $20
No. 3 The endangered species: a symposium. $15
No. 4 Soil-plant-animal relationships bearing on revegetation and land reclamation in Nevada deserts. $15
No. 5 Utah Lake monograph. $15
No. 6 The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. $60
No. 7 Biology of desert rodents. $15
No. 8 The black-footed ferret. $20
No. 9 A Utah flora. $40
No. 10 A reclassification of the genera of Scolytidae (Coleoptera). $20
No. 11 A catalog of Scolytidae and Platypodidae (Coleoptera), part 1: bibliography. $50
No. 12 Research in the Auchenorrhyncha, Homoptera: a tribute to Paul W. Oman. $30

INFORMATION FOR AUTHORS

The *Great Basin Naturalist* welcomes previously unpublished manuscripts pertaining to the biological natural history of western North America. Preference will be given to concise manuscripts of up to 12,000 words.

SUBMIT MANUSCRIPTS to James R. Barnes, Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, Utah 84602. A cover letter accompanying the manuscript must include phone number(s) of the author submitting the manuscript; it must also provide information describing the extent to which data, text, or illustrations have been used in other papers or books that are published, in press, submitted, or soon to be submitted elsewhere. Authors should adhere to the following guidelines; manuscripts not so prepared may be returned for revision.

MANUSCRIPT PREPARATION. Consult Vol. 51, No. 2 of this journal for specific instructions on style and format. These instructions, GUIDELINES FOR MANUSCRIPTS SUBMITTED TO THE GREAT BASIN NATURALIST, supply greater detail than those presented here in condensed form. The guidelines are printed at the back of the issue; additional copies are available from the editor upon request. Also, check the most recent issue of the *Great Basin Naturalist* for changes and refer to the *CBE Style Manual*, 5th edition (Council of Biology Editors, Suite 1200, 230 N. Michigan Avenue, Chicago, IL 60601-5961 USA; $24).

TYPE AND DOUBLE SPACE all materials, including literature cited, table headings, and figure legends. Avoid hyphenated words at right-hand margins. Underline words to be printed in italics. Use standard bond (22 × 28 cm), leaving 2.5-cm margins on all sides.

SUBMIT 3 COPIES of the manuscript. Number all pages and assemble each copy separately: title page, abstract and key words, text, acknowledgments, literature cited, appendices, tables, figure legends, figures.

TITLE PAGE includes an informative title no longer than 15 words, names and addresses of authors, a running head of fewer than 40 letters and spaces, footnotes to indicate change of address and author to whom correspondence should be addressed if other than the first author.

ABSTRACT states the purpose, methods, results, and conclusions of the research. It is followed by 6–12 key words, listed in order of decreasing importance, to be used for indexing.

TEXT has centered main headings printed in all capital letters; second-level headings are centered in upper- and lowercase letters; third-level headings begin paragraphs.

VOUCHER SPECIMENS. Authors are encouraged to designate, properly prepare, label, and deposit high-quality voucher specimens and cultures documenting their research in an established permanent collection, and to cite the repository in publication.

REFERENCES IN THE TEXT are cited by author and date: e.g., Martin (1989) or (Martin 1989). Multiple citations should be separated by commas and listed in chronological order. Use " et al." after name of first author for citations having more than two authors.

ACKNOWLEDGMENTS, under a centered main heading, include special publication numbers when appropriate.

LITERATURE CITED, also under a centered main heading, lists references alphabetically in the following formats:

Mack, G. D., and L. D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. Journal of Wildlife Management 44: 695–700.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Coulson, R. N., and J. A. Witter. 1984, Forest entomology: ecology and management. John Wiley and Sons, Inc., New York. 669 pp.

TABLES are double spaced on separate sheets and designed to fit the width of either a single column or a page. Use lowercase letters to indicate footnotes.

PHOTOCOPIES OF FIGURES are submitted initially with the manuscript; editors may suggest changes. Lettering on figures should be large enough to withstand reduction to one- or two-column width. Originals must be no larger than 22 × 28 cm.

NOTES. If your manuscript would be more appropriate as a short communication or note, follow the above instructions but do not include an abstract.

A CHARGE of $45 per page is made for articles published; the rate for subscribers will be $40 per page. However, manuscripts with complex tables and/or numerous half-tones will be assessed an additional charge. Reprints may be purchased at the time of publication (an order form is sent with the proofs).

FINAL CHECK:

- Cover letter explains any duplication of information and provides phone number(s)
- 3 copies of the manuscript
- Conformity with instructions
- Photocopies of illustrations

(ISSN 0017-3614)

GREAT BASIN NATURALIST Vol. 51, No. 1, March 1991

CONTENTS

The *Great Basin Naturalist* 50-Year Index, Volumes 1–50, 1939–1990. . .
. . . . Jody N. Reid, Richard D. Jensen, and Nathan M. Smith **1–108**

MCZ
LIBRARY
AUG 2[illegible] 1991
HARVARD
UNIVERSITY

THE
GREAT BASIN
NATURALIST

VOLUME 51 № 2 — JUNE 1991

BRIGHAM YOUNG UNIVERSITY

GREAT BASIN NATURALIST

Editor

James R. Barnes

290 MLBM
Brigham Young University
Provo, Utah 84602

Associate Editors

Michael A. Bowers
Blandy Experimental Farm
University of Virginia
Box 175
Boyce, Virginia 22620

Jeanne C. Chambers
USDA Forest Service Research
860 North 12th East
Logan, Utah 84322-8000

Jeffrey R. Johansen
Department of Biology
John Carroll University
Cleveland, Ohio 44118

Paul C. Marsh
Center for Environmental Studies
Arizona State University
Tempe, Arizona 85287

Brian A. Maurer
Department of Zoology
Brigham Young University
Provo, Utah 84602

Jimmie R. Parrish
Department of Zoology
Brigham Young University
Provo, Utah 84602

Editorial Board. Richard W. Baumann, Chairman, Zoology; H. Duane Smith, Zoology; Clayton M. White, Zoology; Jerran T. Flinders, Botany and Range Science; William Hess, Botany and Range Science. All are at Brigham Young University. Ex Officio Editorial Board members include Clayton S. Huber, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications; James R. Barnes, Editor, *Great Basin Naturalist*.

The *Great Basin Naturalist*, founded in 1939, is published quarterly by Brigham Young University. Unpublished manuscripts that further our biological understanding of the Great Basin and surrounding areas in western North America are accepted for publication.

Subscriptions. Annual subscriptions to the *Great Basin Naturalist* for 1991 are $25 for individual subscribers, $15 for student and emeritus subscriptions, and $40 for institutions (outside the United States, $30, $20, and $45, respectively). The price of single issues is $12. All back issues are in print and available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to the Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, UT 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining the *Great Basin Naturalist* through a continuing exchange of scholarly publications should contact the Exchange Librarian, Harold B. Lee Library, Brigham Young University, Provo, UT 84602.

EDITORIAL PRODUCTION STAFF

JoAnne Abel	Technical Editor
Carolyn Backman	Assistant to the Editor
Heidi Larsen	Production Assistant

Copyright © 1991
by Brigham Young University

ISSN 0017-3614
7-91 750 50951

The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

ISSN 0017-3614

Volume 51 | 30 June 1991 | No. 2

Great Basin Naturalist 51(2), 1991, pp. 109–126

EVOLUTIONARY DIFFERENTIATION WITHIN THE NORTHERN GREAT BASIN POCKET GOPHER, *THOMOMYS TOWNSENDII*.
I. MORPHOLOGICAL VARIATION

Mary Anne Rogers[1]

Abstract.—Geographic and nongeographic variation in morphology was examined in *Thomomys townsendii*. A univariate analysis of external and cranial characters from a large population sample (66 adults; fusion of cranial sutures used as aging criteria) was used to assess variation among three adult age classes and between sexes. Only minor variation is apparent among age classes; however, sexual dimorphism is pronounced. Univariate and multivariate techniques were used to analyze external and cranial measurements and pelage characters for adults throughout the species range. These analyses show little to support the seven subspecific designations recognized by Davis (1937). The general pattern is one of homogeneity throughout the range of *Thomomys townsendii*. With the possible exception of *T. t. nevadensis* samples, current subspecies are not defined as morphological units. In fact, differentiation is found among populations within some subspecies. The most apparent pattern seen in these analyses is the divergence between the Humboldt River (including Honey Lake Valley samples) and Snake River systems. These results will be considered with those of a companion paper on the genetic variation in this species to more adequately assess the patterns of differentiation in *Thomomys townsendii*.

Key words: Thomomys townsendii, *pocket gophers, morphological variation, geographic variation, sexual dimorphism.*

For many years pocket gophers of the genus *Thomomys* have been examined and discussed in the context of their tendency to differentiate. In his monograph on *Thomomys*, Bailey (1915) detailed the biology of this "plastic group," including variation in body size and coat color, and correlated environmental factors such as soil color and texture. He noted the correspondence of the limits of many races with physiographic features or climatic areas.

Relationships between the topographic and climatic diversity of California and its numerous forms of pocket gophers were considered by Bailey (1915) and in greater detail by Grinnell (1927). Grinnell cited the fossorial nature of pocket gophers and their relative inability to disperse over land as biological factors affecting isolation and differentiation of gopher populations. He cited unsuitable soils (such as lava flows), rivers, and insufficient food resources characteristic of dry or alkaline areas as environmental factors that isolate populations from one another. Distribution of the different forms often adheres to altitudinal or climatic boundaries, and features distinguishing these races reflect the nature of the habitat in which they are found.

Since these early studies, investigators have continued to focus on defining and understanding morphological variation within the family Geomyidae. A variety of factors has

---

[1] Department of Zoology, Field Museum of Natural History, Chicago, Illinois 60605.

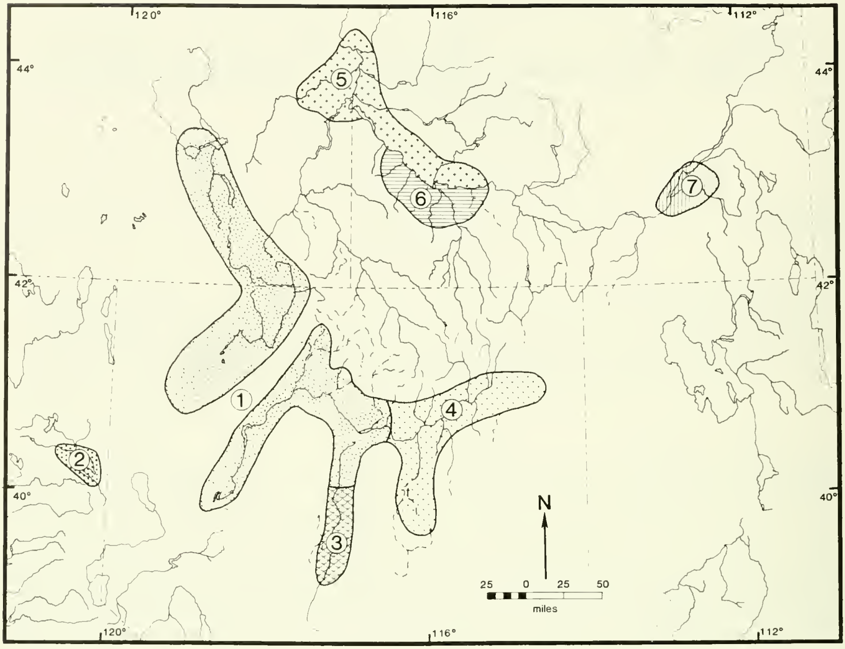


Fig. 1. Map of the present distribution of *Thomomys townsendii* modified from Davis 1937 and Hall and Kelson 1959: 1, *T. townsendii bachmani*; 2, *T. townsendii relictus*; 3, *T. townsendii nevadensis*; 4, *T. townsendii elkoensis*; 5, *T. townsendii townsendii*; 6, *T. townsendii owyhensis*; 7, *T. townsendii similis*.

been discussed as possible determinants of the patterns of variation seen among populations, subspecies, and species of pocket gophers (Davis 1938, 1940, Ingles 1950, Thaeler 1968, Smith and Patton 1980, 1988, Patton and Brylski 1987, Patton and Smith 1989). Davis (1938) found size in *Thomomys* to be directly correlated with soil conditions and inversely correlated with elevation. In addition to establishing that larger forms of *Thomomys* are found in deeper soils at lower elevations, Davis also found that larger gophers are more sexually dimorphic. A recent study by Patton and Brylski (1987) demonstrates that body size and sexual dimorphism in pocket gophers are strongly influenced by the nutritional value of their food, while variation in shape is more likely to reflect genetic changes.

Davis (1937) examined morphological differentiation across the range of *T. townsendii*. This species of pocket gopher is discontinuously distributed through northeastern California, northern Nevada, southeastern Oregon and southern Idaho (Fig. 1), where its range is restricted to deep lacustrine or fluviatile soils. Discontinuities in the distribution reflect barriers in the form of expanses of unsuitable desert soils and lava flows and the presence of competing gopher species. Davis (1937) identified these features in his analysis of *T. townsendii* and indicated their importance in influencing the differentiation of the species into the seven subspecies recognizable on the basis of morphological characters.

This study examines variation in external and cranial characters both within and among populations of *Thomomys townsendii* and compares these patterns to the results of Davis's study. In a companion paper (Rogers 1991) results of genetic analyses are also considered. To help explain the resulting patterns of differentiation, the analysis draws from information regarding the biogeographic history of the area, aspects of gopher population biology, and evolutionary relationships within the genus *Thomomys*. The morphological differentiation and taxonomy outlined by Davis (1937) are reexamined in the context of patterns of morphological and genetic differentiation shown in these analyses.

MATERIALS AND METHODS

Aging Criteria

An age category, based upon the degree of fusion of the basioccipital/basisphenoid and the supraoccipital/exoccipital sutures of the skull (Hoffmeister 1969, Honeycutt and Schmidly 1979, Patton et al. 1979), was assigned to each of 628 individuals examined. Each suture was scored on a scale of 1 to 3, with 3 being the most complete stage of fusion. The scores for the two sutures of each individual were then summed to arrive at an age-class value for each individual. The utility of these aging criteria was tested by examining the correspondence of the age categories to molt stage and body size. The large sample from Honey Lake Valley was used to minimize any geographic component of the variation. Males and females were treated separately due to the marked sexual dimorphism often found in geomyids (Merriam 1895, Bailey 1915, Hoffmeister 1969, Honeycutt and Schmidly 1979, Patton et al. 1979). For analyses of interpopulation variation the remaining population samples were also categorized based on cranial suture criteria. Only specimens judged to be adults were used in subsequent morphometric analyses, with the exception of juveniles in adult pelage, which were used only in the analysis of pelage coloration.

Analysis of Morphological Characters

A total of 477 adult *Thomomys townsendii* were measured for analysis of morphometric variation. In most instances localities were pooled based on geographic proximity in order to increase sample sizes. The resulting 31 composite localities are shown in Figure 2, and their component localities are listed in the Appendix. All localities were included in analyses of interpopulation variation. The two Honey Lake Valley localities were used to examine aspects of nongeographic variation.

Four external and 28 cranial measurements were recorded for each individual. Total length (TOL), tail length (TAL), hind foot length (HFL) and ear height (EH) were recorded directly from the skin tag of each specimen. Cranial dimensions were measured with dial calipers. These measurements, illustrated in Figure 3, are as follows: occipito-nasal length (ONL), basilar length of Hensel (BAL), zygomatic breadth (ZB), mastoid breadth (MASB), interorbital constriction (IOC), rostral length (RL), nasal length (NL), rostral width (RW), diastema length (DIAS), palatal width (PALW), bullar length (BUL), rostral depth (RD), cranial depth (CRD), frontal length–total (FRLT), width foramen magnum (WFM), height foramen magnum (HFM), frontal length–medial (FRLM), dorsal length orbit (DLO), ventral length orbit (VLO), braincase depth (BRCD), width premaxillary tongue (PMXT), premaxillary width (PMXW), length maxillary mortise (MAXM), tooth row length (TRL), depth jugal (DJUG), length anterior edge jugal (LAJ), breadth zygomatic arch (BZA), and distance of procumbancy (DPRO).

A subset of 128 specimens in adult pelage were selected for color analysis. These individuals represented both the geographic range (Appendix) and the variety of pelage colors visible among the available samples for each of the seven subspecies. Albino and melanic individuals were excluded from the analysis. To increase sample size, the 31 localities used in the morphological analyses were grouped by geographic proximity into 13 units and assigned alphabetical designations, A–M.

Variation in mid-dorsal pelage coloration was quantified using a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment (for details of colorimetric techniques see Bowers 1956, Selander and Johnston 1967, and Genoways 1973). For each animal, trichromatic coefficients (x, y, and z) were derived from curves of percentage reflectance. Values for percent brightness (= value), dominant wavelength (= hue), and percent excitation purity (= chroma) were calculated from these coefficients.

Statistical Methods

The Statistical Package for the Social Sciences (SPSS, Nie et al. 1975), versions of

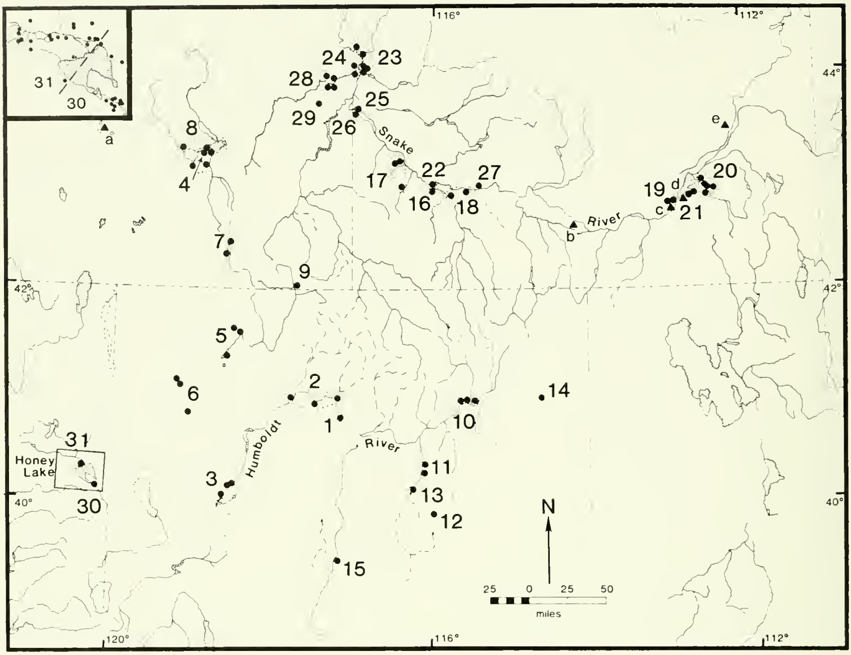


Fig. 2. Map of samples for morphological analysis (circles) and sites from which fossil material of *Thomomys townsendii* has been found (triangles). Inset shows detail of distribution of localities within the Honey Lake Valley. Locality information for recent material is given in the Appendix. Fossil localities are as follows: (a) Fossil Lake, Lake Co., Oregon (early–mid-Wisconsin; Elftman 1931, Allison 1966); (b) Wilson Butte Cave, Jerome Co., Idaho (late Wisconsin to Recent; Gruhn 1961); (c) American Falls, Power Co., Idaho (Sangamonian; Gazin 1935, Hopkins et al. 1969); (d) Rainbow Beach, Power Co., Idaho (late Wisconsin; McDonald and Anderson 1975); (e) Wasden Site, Bonneville Co., Idaho (late Wisconsin to Recent; Guilday 1969).

ANOVA, and discriminant function analysis were utilized for the analyses. Matrices of F values generated by discriminant function analyses of cranial morphology were clustered using the NTSYS program of Rohlf et al. (1980) as edited for use at University of California, Berkeley, by T. Duncan. Cranial and external data were analyzed using the University of California, Berkeley, computing facilities. Analyses of the three color variables were performed on the Amdahl 470 at the University of Chicago Computation Center.

In establishing aging criteria, t tests were used to compare the mean body weight and mean total length of adult and juvenile age classes from the Honey Lake Valley sample. The Honey Lake Valley adults (41 males, 25 females) were examined to assess age and sex components of intrapopulation variation in the 28 cranial and 4 external characters. Two-way ANOVA tables were calculated for each of the 32 variables to determine the extent of variation among adult age classes, to assess secondary sexual variation, and to examine interaction effects.

The extent and nature of variation in each of the 32 morphological characters across the range of *T. townsendii* were examined using one-way ANOVAs. In addition to the statistics generated for the intrapopulation analyses, homogeneous subsets of samples were established by Duncan's multiple range tests ($\alpha = .05$). All adult specimens, representing 31 localities, were utilized for the interpopulation

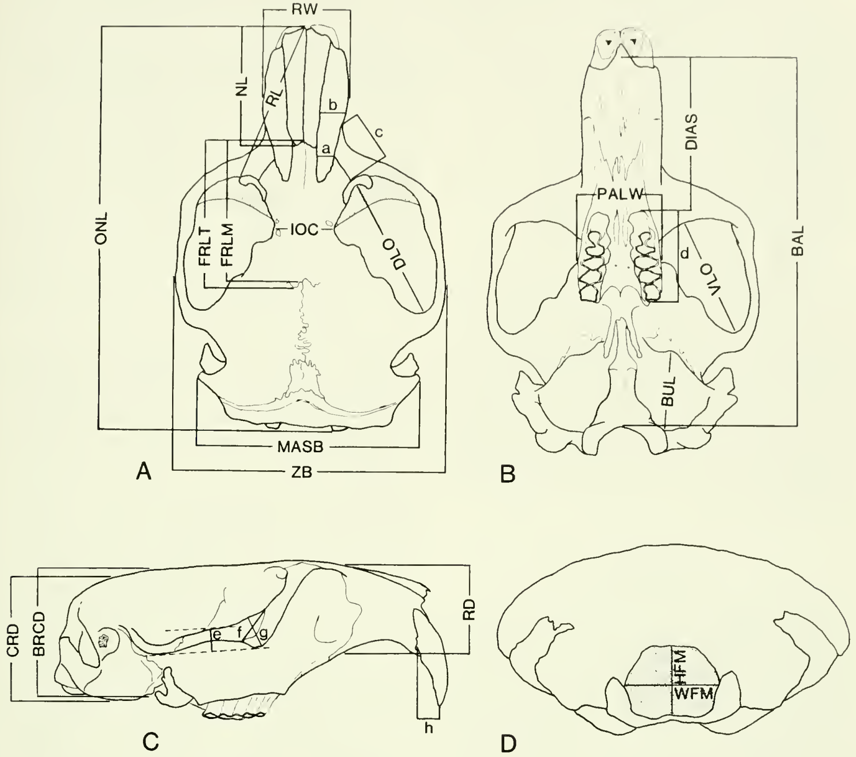


Fig. 3. Twenty-eight cranial dimensions utilized in morphological analysis. Abbreviations correspond to the following dimensions: ONL, occipito-nasal length; BAL, basilar length of Hensel; ZB, zygomatic breadth; MASB, mastoid breadth; IOC, interorbital constriction; RL, rostral length; NL, nasal length; RW, rostral width; DIAS, diastema length; PALW, palatal width; BUL, bullar length; RD, rostral depth; CRD, cranial depth; FRLT, frontal length–total; WFM, width foramen magnum; HFM, height foramen magnum; FRLM, frontal length–medial; DLO, dorsal length orbit; VLO, ventral length orbit; BRCD, braincase depth. Lowercase letters correspond to the following dimensions: a, width premaxillary tongue (PMXT); b, premaxillary width (PMXW); c, length maxillary mortise (MAXM); d, tooth row length (TRL); e, depth jugal (DJUG); f, length anterior edge jugal (LAJ); g, breadth zygomatic arch (BZA); h, distance of procumbancy (DPRO).

comparisons. Since some localities were not represented by both male and female specimens, a total of 30 samples of females and 24 samples of males were analyzed. For clarification, presentation of the results of these analyses may refer to the broad alphabetical locality designations described above, but morphological analyses were performed on the smaller population units.

Multivariate techniques were performed on the 28 cranial measurements for the 30 female and 24 male population samples using discriminant function analysis. Individuals with missing values for any of the variables were excluded from the calculations. A stepwise method was chosen for the entry of the variables into the analysis, using the maximum Mahalonobis distance as the selection criterion. A matrix of *F*-ratios for each pair of groups was calculated after each step, testing the significance of the Mahalonobis distance between groups. Discriminant function coefficients for each variable and discriminant scores for each individual were calculated. Individuals were plotted two-dimensionally based on discriminant function (DF) 1 and DF2 scores with group centroids indicated. Classification information was provided, indicating the a posteriori probabilities of an individual belonging to its actual group and to the next closest group. Males ($n = 211$) and females ($n = 266$) were treated separately in all univariate and multivariate analyses.

Pelage data (values obtained for brightness, wavelength, and purity) were subjected to similar univariate and multivariate analyses, except that four different grouping schemes were employed in order to define regional patterns of pelage variation. Data were grouped by locality (1–31), by locality groups (A–M), by subspecies, and by major geographic region (Humboldt River, Snake River, Honey Lake Valley). Each grouping scheme was treated separately for each analysis.

RESULTS

Aging Criteria

Results obtained from Honey Lake Valley animals indicate that the adult age category, based on cranial suture criteria, is well differentiated by body weight and total length from the juvenile category. *T* tests show the two age categories (classes 1–3 and 4–6) differ significantly ($P < .05$) in body weight and total length. Examination of molt stages of individuals from Honey Lake Valley shows that the majority (96%) of the individuals categorized as having adult crania (age classes 4, 5, and 6) were in full adult pelage. "Adult" pelage does not necessarily correspond to reproductive maturity or fully fused sutures, as the juvenile pelage is replaced within the first several months of life (Howard and Childs 1959) and some individuals seem to be breeding before reaching full adult pelage. It does, however, represent a chronological stage that is, in this case, completed by the time the individual has reached adult stages of cranial development.

Intrapopulation Variation

ANALYSIS OF AGE AND SEX EFFECTS.—Analyses of the Honey Lake sample suggest that variation among the three adult age classes of *Thomomys townsendii* is negligible, whereas sexual dimorphism is pronounced. ANOVA results indicate that only TRL ($P < .01$) and LAJ ($P < .05$) show significant differentiation among age classes. The overall lack of appreciable age effect across the 32 characters indicates that there are only minor differences in the dimensions of the skull or body that correspond to suture fusion classes. However, there is significant ($P < .01$) variation between the sexes for all but four of the characters examined: EH, IOC, HFM, and PMXT. Only TRL shows a significant ($P < .05$) interaction effect between age and sex. It is important to note that the significant age effect found in TRL is dependent on the sex of the animal.

Due to the homogeneity among adult age classes, analyses of geographic character trends were performed without distinguishing among them. However, since the majority of the characters analyzed do indicate secondary sexual variation, the sexes were treated separately here as in other studies (Patton et al. 1979, Smith and Patton 1988). Adult male skulls can become larger and more heavily ridged than female skulls in instances of pronounced sexual dimorphism and can therefore introduce ontogenetic variation that could confuse the evaluation of adult skull morphology (Merriam 1895, Bailey 1915, Grinnell 1935). Since characters of the more uniform female skull are more reliable for phylogenetic interpretations, females have often been the focus of morphological descriptions (Grinnell 1931, 1935, Davis 1937). Discussion of the results of some analyses in this study will also emphasize females.

Interpopulation Variation

ANALYSIS OF CRANIAL AND EXTERNAL CHARACTERS.—Univariate analyses of each of the 32 variables examined across the 31 localities reveal significant ($P < .001$) levels of variation among populations for both males and females. Despite overall significance of variation in each of these characters, inspection of the means and ranges across the populations reveals general homogeneity and little subspecific or regional cohesiveness. Based on the F-ratios of the variables, characters such as NL, CRD, PMXT, and LAJ suggest clearer population differentiation. The distinction between populations may be more apparent for these characters, but in some cases it reflects differentiation between populations of the

TABLE 1. Relative contributions of the first 11 discriminant functions of the analyses of 26 cranial characters.

	Females			Males		
DF	% variance	Cum. %	Eig. val.	% variance	Cum. %	Eig. val.
1	30.24	30.24	7.540	39.89	39.89	9.453
2	15.96	46.19	3.979	14.44	54.33	3.422
3	11.55	57.74	2.880	8.70	63.02	2.061
4	9.18	66.93	2.290	7.32	70.34	1.734
5	5.63	72.56	1.405	6.12	76.46	1.451
6	4.20	76.76	1.048	5.08	81.55	1.204
7	3.73	80.49	0.929	3.66	85.21	0.868
8	3.66	84.14	0.912	2.85	88.06	0.675
9	2.81	86.95	0.700	2.77	90.83	0.656
10	2.51	89.46	0.627	1.98	92.81	0.470
11	2.16	91.63	0.540	1.71	94.52	0.406

same currently recognized subspecies. NL values for populations of *Thomomys townsendii townsendii*, for example, encompass nearly the full range of values for the 30 female samples. In addition, subsets established by Duncan's multiple range tests indicate a large amount of overlap among the 31 samples, for all variables. In ranking the population means for each variable, no geographic trend is apparent; rather, a pattern of interdigitation of representatives from different geographic and subspecific units emerges. In instances where populations are ranked into nonoverlapping groups, populations of a given subspecies or geographic region are likely to be found in each group. For example, populations of *T. t. townsendii*, *T. t. elkoensis*, and *T. t. bachmani* are found in each of two nonoverlapping subsets that represent the highest and lowest values for CRD.

Discriminant function analysis was ultimately performed using 26 of the 28 cranial characters in order to maximize sample size. By removing LAJ and DPRO, characters that were often represented by missing values, the sample size increased with little effect on the ability to differentiate among the 31 populations. The discriminating power of the 26 cranial variables is comparable for the two sexes. Eigenvalues and percent variation for each discriminant function are given in Table 1. For females, the first 10 functions are needed before roughly 90% of the existing variance is used to distinguish between the populations. The first nine functions are necessary in the discrimination of males. Among females, the main contributing variables for DF1 are ONL, BAL, RL, NL, and CRD. Those for DF2 are RL, NL, RD, MAXM, and DJUG.

Ninety-six percent of specimens of each sex are correctly classified by the a posteriori probability of group membership of each specimen. Misclassified individuals are often placed in populations of another subspecies. While Snake River individuals are, with one exception, classified into other populations of that region, Humboldt River animals are sometimes placed in one of the Honey Lake Valley populations and vice versa.

The two-dimensional plots of individual scores show considerable interpopulation overlap in scores for DF1 and DF2 (see Figs. 4, 5). Despite this remarkably low amount of differentiation, discriminant function analyses succeed in revealing some patterns. Along DF1 Snake River populations form a more cohesive unit than that seen in the ANOVA results. A broad range in values is seen in the Humboldt River representatives. In fact, the range of coefficients found within *T. t. bachmani* alone (populations 1–9; see map, Fig. 2) nearly encompasses the DF1 values of the entire Humboldt River region. Some of the variation seen within *T. t. bachmani* is due to the deviation of populations 4 and 8 (Malheur Lake and Narrows region of Oregon) from the other samples of that subspecies (extreme southeastern Oregon, Quinn River, and Humboldt River areas). Also noteworthy is the similarity of Honey Lake Valley (*T. t. relictus*) populations in DF1 to the populations of southeastern Oregon and Nevada.

Individual scores show less obvious regional differentiation in DF2 than in DF1. The patterns seen for this function are subtle and involve within-subspecies differentiation; they are similar for both males and females. Nearly the full range of DF2 is found among

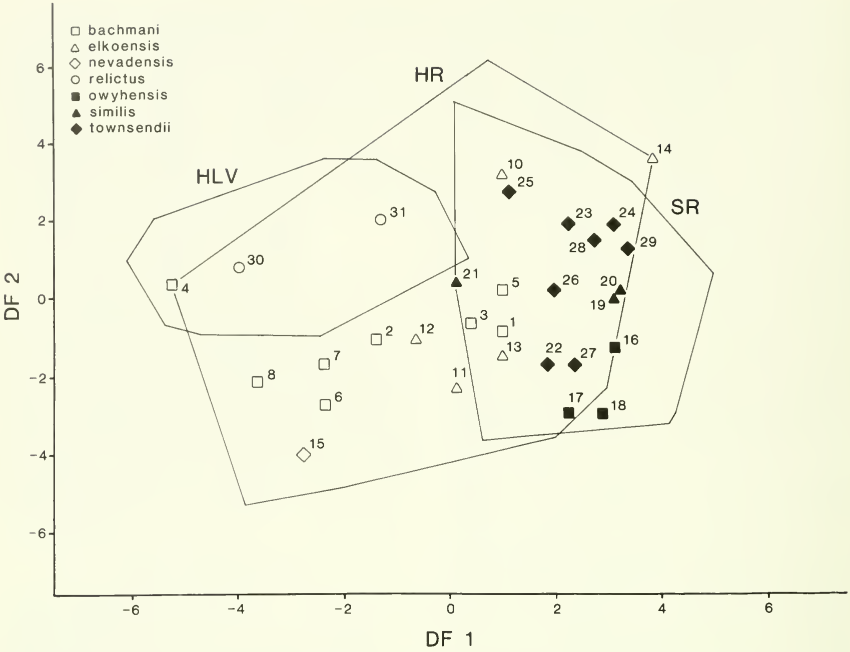


Fig. 4. Polygons encompassing individual scores for DF1 and DF2 for females from Honey Lake Valley (HLV), Humboldt River (HR), and Snake River (SR). Population centroids are indicated by numbered symbols. DF1 and DF2 represent 30.2% and 16.0% of the variance, respectively.

the Humboldt River animals. Honey Lake Valley animals fall into the same range as western *T. t. townsendii* populations (23–26, 28, 29) from along the Snake River. As seen in the ANOVA results, eastern populations (22 and 27) of *T. t. townsendii* are distinct from the majority of the samples of that subspecies. The easternmost populations of *T. t. elkoensis* (10 and 14) are also differentiated from the remainder of that subspecies. The significance of these deviations from subspecific and regional cohesiveness will be discussed later.

Matrices of *F*-ratios generated with the final steps of the discriminant function analyses were used to illustrate interrelationships of the 31 populations. A UPGMA phenogram summarizing these ratios was generated for each sex (Figs. 6, 7). The phenograms provide a summary of the contributions of all discriminant functions. The patterns mentioned above for DF1 and DF2 are apparent: (1) subspecific and regional units are not readily distinguishable due to a large degree of overlap, (2) Snake River populations show a tendency toward cohesiveness, and (3) most intra-subspecific deviations in character trends are geographic subunits segregated in DF1 (populations 4 and 8 of *T. t. bachmani*) and DF2 (populations 22 and 27 of *T. t. townsendii*, populations 10 and 14 of *T. t. elkoensis;* see map, Fig. 2). In addition, populations of *T. t. relictus* and *T. t. nevadensis* and populations 4 and 8 of *T. t. bachmani* are well differentiated from the remaining groups based on *F*-ratios.

Analysis of pelage coloration.—The means and ranges of the three color variables for each locality are listed in Table 2. Discriminant function analyses of localities and locality groups show a substantial degree of overlap in coloration across the range of *Thomomys townsendii*. In the analysis of locality

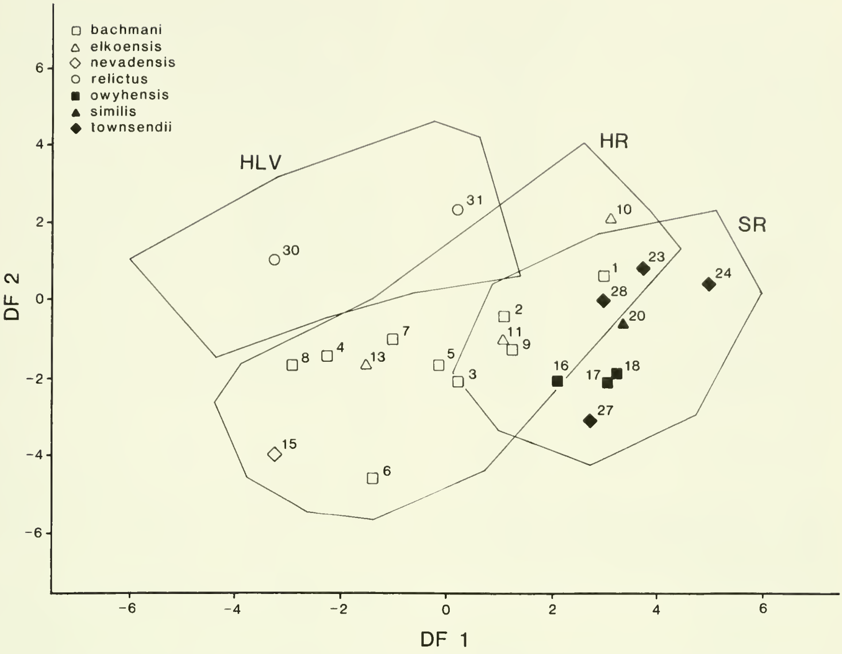


Fig. 5. Polygons encompassing individual scores for DF1 and DF2 for males from Honey Lake Valley (HLV), Humboldt River (HR), and Snake River (SR). Population centroids are indicated by numbered symbols. DF1 and DF2 represent 39.9% and 14.4% of the variance, respectively.

groups, only 29.69% of the cases were correctly classified using the three color variables as discriminators. The misclassified individuals were frequently placed into locality groups of other subspecies or into another major geographic region. Of the total variance, 73.97% is associated with the first discriminant function, which is most strongly represented by brightness. The contribution of brightness is similar in the discriminant function analyses at all levels.

The distribution of DFI scores is graphically superimposed on the means and ranges for brightness in Figure 8, illustrating the concordance of the DF1 scores and brightness values and highlighting the contribution of brightness to DF1. Some separation along the function is apparent. For example, while populations of *T. t. elkoensis*, *T. t. similis*, and the eastern population (J) of *T. t. townsendii* are similar in ranges of DF1 values and group means, they do not overlap with the values for *T. t. nevadensis*. However, there is a range of overlap along DF1, corresponding to a range of brightness values (10–15%), within which all locality groups are represented. If one were to characterize, in general terms, the pelage coloration at the subspecific level, *T. t.elkoensis*, *T. t. similis*, *T. t. owyhensis*, and most *T. t. townsendii* are relatively dark (locality means for brightness, $\bar{x}$ = 9–11%); *T. t. bachmani*, *T. t. relictus* and some *T. t. townsendii* are brighter ($\bar{x}$ = 11.5–14%); *T. t. nevadensis* is the brightest ($\bar{x}$ = 17%).

If variation in pelage color is considered in the context of subspecific ranges or broader geographic units, there is a somewhat clearer pattern of differentiation from what is seen at the population level. Discriminant function analyses performed on localities grouped by subspecies or regions show increased discriminating power (percent correctly classified: 39.84 and 50.00, respectively).

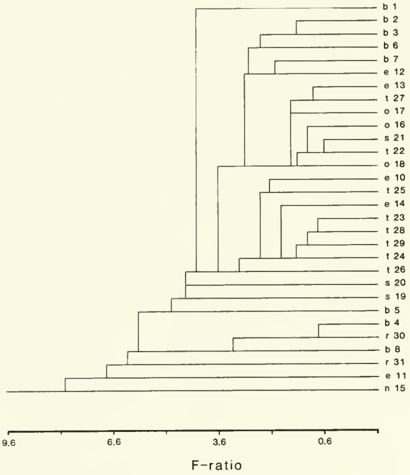


Fig. 6. UPGMA phenogram based on *F*-ratios from discriminant function analysis of females. Lowercase letters refer to subspecific designations and are followed by population numbers.

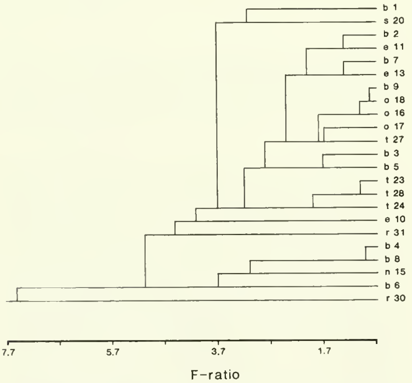


Fig. 7. UPGMA phenogram based on *F*-ratios from discriminant function analysis of males. Lowercase letters refer to subspecific designations and are followed by population numbers.

Analyses of variance confirm the relative importance of brightness in determining geographic trends in coloration. Of the color variables examined, brightness shows the most significant level of variation at every level of analysis. Amounts of between-group variation for wavelength and purity become insignificant ($P > .05$) when examined at the subspecific and/or regional levels. The homogeneous subsets of locality groups established by Duncan's multiple range tests (Fig. 9) again show *T. t. nevadensis* of central Nevada as clearly differentiated from all other populations. The other subsets encompass populations from different subspecies and from different geographic regions. When the subspecies are compared as units, *T. t. elkoensis*, from the eastern Humboldt River drainage, is grouped with *T. t. similis* from the Snake River. Comparison of the three geographic regions shows that animals from Honey Lake Valley and the Humboldt River are, in general, more similar in brightness values to each other than either is to the Snake River animals.

Color variants.—*Thomomys townsendii* occurs in a melanistic form as well as in the range of color morphs described above (Bailey 1915, Davis 1937). In addition, in this study one pure white individual was trapped at 6 mi. SE Murphy, Owyhee Co., Idaho. Melanic gophers formed a larger component of the specimens examined, being found in three of the seven subspecies with the following frequencies: *T. t. bachmani*, 8.25%; *T. t. relictus*, 0.57%; *T. t. townsendii*, 4.69%. In addition to these pelage morphs, a white "blaze" was frequently seen on the heads of individuals from two subspecies: *T. t. relictus*, 17.61%; *T. t. owyhensis*, 17.95%.

Discussion

The results of this study of *Thomomys townsendii* have shown general homogeneity in external, cranial, and pelage characters across a very broad and disjunct geographic range. Pocket gophers have long been noted for their adaptation to the soils they inhabit, especially in the differentiation of pelage coloration and body size (Grinnell 1927, Davis 1938, Ingles 1950). More recently, an emphasis has been placed on the role of the nutritional value of available food in determining body size (Smith and Patton 1980, 1988, Patton and Brylski 1987). The homogeneity seen in *T. townsendii* body size might be explained by the preference of this species for the deep lacustrine soils of the Great Basin. However, without further investigations it is difficult to

TABLE 2. Means and ranges for color variables brightness, wavelength, and purity.

Locality	*n*	Brightness	Wavelength	Purity
1	7	10.98 (7.26–14.28)	582.14 (580–583)	15.94 (5.98–24.95)
2	4	14.15 (11.30–17.04)	582.50 (582–583)	25.18 (20.62–27.69)
3	4	14.37 (11.96–17.20)	582.00 (581–583)	20.08 (16.70–22.39)
5	6	12.55 (10.38–14.22)	581.17 (580–582)	15.19 (10.10–17.26)
6	4	16.72 (15.41–17.72)	580.50 (580–581)	22.89 (21.71–24.03)
7	2	14.93 (12.93–16.92)	581.00 (581–581)	20.95 (19.36–22.55)
8	10	12.49 (9.91–14.66)	582.90 (582–584)	21.11 (15.94–27.37)
9	1	10.82 —	582.00 —	14.01 —
10	10	9.20 (7.02–11.31)	580.80 (578–582)	12.42 (3.33–26.69)
11	6	8.96 (7.69–10.96)	582.67 (582–584)	12.16 (6.61–16.87)
12	1	11.12 —	581.00 —	15.48 —
13	1	9.33 —	582.00 —	14.98 —
15	11	17.02 (14.15–20.19)	582.09 (581–584)	23.37 (18.84–27.80)
16	5	9.88 (8.66–12.44)	583.40 (583–584)	17.84 (15.31–24.20)
17	7	11.04 (9.42–14.26)	582.71 (581–584)	21.07 (16.15–29.24)
18	2	13.08 (12.29–13.87)	583.00 (583–583)	25.34 (20.18–30.50)
19	5	9.44 (7.24–10.88)	582.40 (581–584)	17.27 (10.63–20.83)
20	9	9.18 (6.83–10.75)	582.56 (580–586)	11.76 (5.31–18.76)
21	1	9.18 —	582.00 —	19.05 —
22	1	6.87 —	583.00 —	6.78 —
23	5	11.82 (9.85–14.16)	581.80 (581–583)	19.05 (14.67–25.62)
24	1	13.04 —	584.00 —	28.21 —
25	2	8.35 (7.83– 8.86)	581.50 (581–582)	19.90 (18.36–21.44)
27	3	9.94 (7.58–11.18)	583.33 (583–584)	21.23 (14.65–29.30)
28	5	11.43 (10.72–12.22)	582.20 (581–583)	15.85 (12.87–19.42)
30	5	13.73 (11.78–14.91)	581.20 (580–582)	19.03 (16.44–21.57)
31	10	13.76 (11.97–14.91)	582.20 (581–583)	20.30 (17.35–25.04)

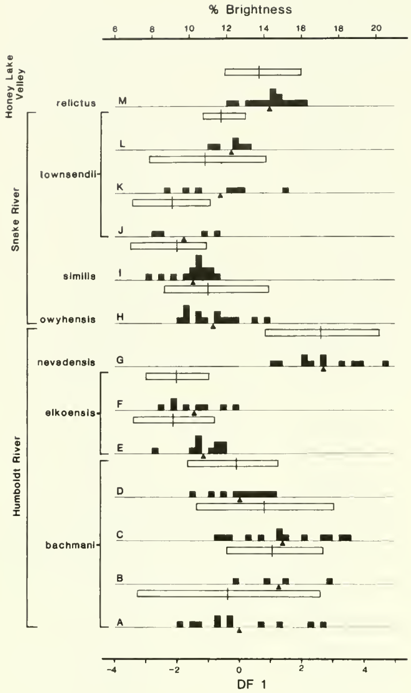


Fig. 8. Plot of individual scores for DF1 from color analysis and group ranges in % brightness values. Solid bars represent DF1 scores; triangles indicate group centroids. Open bars represent range in % brightness values; vertical lines indicate group means. DF1 represents 74.0% of the variance.

say whether the pattern seen is in response to color or other properties of the soil, quality of available food, isolation from other populations, or other influences. The pattern of morphological homogeneity seen in *T. townsendii* should be noted in contrast to the cranial differentiation demonstrated between subspecies or genetically defined intraspecific units in *Thomomys bottae* (Smith et al. 1983, Smith and Patton 1988) and in *Geomys bursarius* (Honeycutt and Schmidly 1979).

In 1937 Davis modified the status of the three subspecies of *Thomomys townsendii* recognized at the time. From his analysis of geographic variation in cranial and external morphology, he concluded that

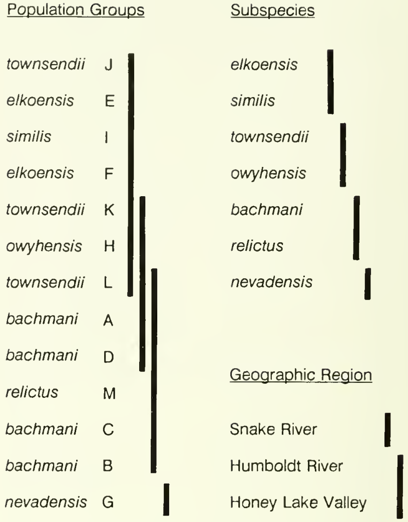

Population Groups
townsendii J
elkoensis E
similis I
elkoensis F
townsendii K
owyhensis H
townsendii L
bachmani A
bachmani D
relictus M
bachmani C
bachmani B
nevadensis G
Subspecies
elkoensis
similis
townsendii
owyhensis
bachmani
relictus
nevadensis
Geographic Region
Snake River
Humboldt River
Honey Lake Valley

Fig. 9. Homogeneous subsets based on brightness. Vertical bars represent homogeneous subsets determined by Duncan's multiple range tests for each of the three color variables. Pairs of population group means were compared and placed in a subset if the means were not significantly different at the α = .05 level. Letters refer to population group designations.

> 7 distinct major centers of differentiation can be recognized, the population in each of which is fairly homogeneous and distinct from any other (Davis 1937:148).

Davis based his subspecific designations on the differentiation of characters or suites of characters across geography. In this study most of the same characters were analyzed; yet the results do not reveal consistent trends corresponding to subspecific units.

However, Davis (1937) also discussed variation within some of the subspecies he recognized. For example, within *T. t. bachmani*, animals from Quinn River and the Little Humboldt River differed from individuals taken along the Humboldt River between Lovelock and Battle Mountain. Davis noted that eastern populations of *T. t. townsendii* and *T. t. owyhensis* were "indistinguishable" externally and occupied similar soil types but that they were distinct in qualitative features of the cranium. Between subspecies two trends in cranial structure were apparent: *T. t. bachmani* was intermediate between

T. t. relictus and *T. t. nevadensis*, and *T. t. similis* was intermediate between *T. t. townsendii* and *T. t. elkoensis*.

Some of the analyses of the present study also suggest both variation within subspecies and similarities to other subspecies which, together, contribute to the homogeneity seen in *T. townsendii*. For instance, while populations of *T. t. bachmani* are very homogeneous in pelage characteristics, cranial analyses showed some differentiation among these samples, the northern populations (4 and 8) being the most divergent (DF1, also reflected in *F*-ratios). The eastern representatives of *T. t. townsendii* consistently deviate from the other populations of the subspecies. While these populations (22 and 27) are not especially distinctive on DF1 of the cranial analyses, they segregate from the other *T. t. townsendii* populations along DF2 and in the summary of the discriminant function analyses as shown by *F*-ratios. The color analysis represented them as the darkest of the Snake River populations and, again, segregated from the northwestern *T. t. townsendii* populations.

Cranial analyses also expose differentiation within *T. t. elkoensis* between the northeastern populations (10 and 14) and those to the south (11, 12, and 13). These populations are distinguished along DF2, the scores for populations 10 and 14 being very similar to those of the Snake River populations. Davis (1937) referred to the affinity between northeastern *T. t. elkoensis* and *T. t. similis* of the Snake River system in the context of the potential link between the two river systems. However, he called them "structurally" similar without detailing the characters involved. Pelage characters show *T. t. elkoensis* to be more cohesive as a subspecies, but they are the darkest of the Humboldt River populations and, again, more like the Snake River animals, possibly in response to some of the environmental factors discussed earlier. Because color analyses were not performed on soil samples in this study, an examination of any adaptive tendency for pelage to match background soil cannot be undertaken. However, Great Basin vegetation zones and the factors that determine these provide an interesting comparison.

The distribution of *Thomomys townsendii* occurs primarily in two of the vegetation zones of the Intermountain Region as described by Cronquist et al. (1972). These are the Shadscale Zone and the Sagebrush Zone. Of these two plant communities, shadscale is more tolerant of saline soils and low moisture conditions. The distribution of shadscale communities in the northern Great Basin is nearly identical to the distribution of the *T. townsendii* populations that exhibit bright pelage. The distribution of the darker populations, including *T. t. elkoensis* and *T. t. similis* samples, falls in the Sagebrush Zone, which probably corresponds to less saline, moister, and therefore darker soils. It is also interesting to note that the eastern *T. t. townsendii* and some *T. t. owyhensis* samples were collected near one of the transitions between these two vegetation zones and therefore may also have come from darker soils.

Although the patterns seen in the morphological analyses are similar to some that Davis found, the characters on which these trends are based are not necessarily the same in both studies. For example, one of the variables contributing strongly to differentiation within *T. t. bachmani* in the discriminant function analysis is NL, but in Davis's study nasal length contributes to the cohesiveness of *T. t. bachmani* as a unit.

Of the areas of differentiation that Davis recognized, the one represented by *T. t. nevadensis* is the most consistently distinguished based on morphological criteria in this study. Although the pattern of overlap with other subspecies persists in the results of all analyses, the *T. t. nevadensis* sample at Austin is the most divergent in the discriminant function and color analyses.

Beyond differentiation into seven subspecies, Davis recognized other trends in *T. townsendii*. He divided *T. townsendii* into two groups based on the breadth of the dorsal surface of the premaxillae. The populations of the Snake River Plain comprised a narrow rostrum group, and those of Honey Lake Valley and the Humboldt River drainage had broader rostra. The present study has also shown differentiation between the two regions representing the Snake River and Humboldt River drainages. However, based on analyses of RW, PMXW, and PMXT, no segregation into broad and narrow rostrum groups is apparent. It is important to note the concordance between Davis's results and this study in placing Honey Lake Valley populations within the Humboldt River region. Cranially, *T. t. relictus* is most similar to *T. t. nevadensis* and northern populations of *T. t. bachmani* along DF1 and in the *F*-ratio phenogram; they are not substantially differentiated from other Humboldt River animals along DF2. In color, they are also intermediate relative to Humboldt River populations.

Multivariate analyses of cranial characters provide the clearest differentiation between regions, showing some overlap but also considerable segregation along DF1, with the Snake River samples exhibiting a narrower range of DF1 values relative to the Humboldt River populations. None of the measurements relating to rostral width contributes importantly to DF1, although length-related characters do, including RL and NL. In the discriminant function analyses for cranial characters, most individuals were correctly classified into their respective populations. The placement of the misclassified individuals suggests similarities between the Honey Lake Valley and Humboldt River populations and greater differentiation of the Snake River populations. In contrast, the color analysis shows a good deal of overlap in pelage coloration of animals from the three regions. Individuals were classified into their respective subspecific units only 40% of the time when the classification was based on pelage characters, and the misclassified cases were often placed into another geographic region.

Animals from the Humboldt River drainage are more diverse morphologically than those of the Snake River populations. The Humboldt River DF1 values for the cranial analyses are broadly scattered along that axis. Brightness values for these populations range from among the darkest to the brightest known for the species. Although both regions include populations that are geographically well separated from one another, Snake River populations have somehow maintained greater morphological homogeneity. There could be a strong environmental component to this pattern in the form of quality of soil and food resources. In addition, the physiographic history and colonization of the two areas may have been sufficiently different to result in the varying degrees of regional differentiation seen today. These possibilities are considered further in a companion paper (Rogers 1991).

Fossil evidence suggests that in relatively recent times these pocket gophers may have been distributed along more of the Snake River basin than they are today. Fossil remains of *T. townsendii* and related forms are rare and known only from the northern part of the *townsendii* distribution (see Fig. 2). *Thomomys scudderi* and *Thomomys vetus* are both known from Wisconsin deposits at Fossil Lake, Oregon (Hay 1921, Davis 1937). Both taxa have been regarded as conspecific with *townsendii* or related to it. Elftman (1931) recognizes fossils from this area as *T. townsendii*. Davis (1937) considered *T. scudderi* more similar to *bottae* and felt *T. vetus* was a *townsendii* relative. Fossils assigned to *T. townsendii* have been found in Oregon at Fossil Lake (early–mid-Wisconsin; Elftman 1931, Allison 1966, Grayson 1982), in Idaho along the central and eastern Snake River Plain at American Falls (Sangamonian; Gazin 1935), Rainbow Beach (Wisconsin; McDonald and Anderson 1975), Wasden Site (Wisconsin to Recent; Guilday 1969), and Wilson Butte Cave (Wisconsin to Recent; Gruhn 1961). Three of these fossil records (Fossil Lake, Wilson Butte Cave, and Wasden Site) are outside the present range of *T. townsendii* (see maps, Figs. 1, 2). Due to the nature of the fossil materials (often only teeth or skull fragments), this evidence establishes, at best, that "*townsendii*-like" animals occurred during the late Pleistocene in the Snake River Plain and to the west at Fossil Lake, Oregon.

In summary, the results of this study do not lend support to the seven subspecific designations established by Davis (1937). There are differences among populations within current subspecies and similarities between populations of different subspecies in cranial and pelage analyses. These patterns suggest some validity in distinguishing between the populations of the two river drainage systems and some weakness in recognizing seven subspecific units. Within each river system more localized differentiation can be shown, such as the marked divergence of the Austin sample, but it is subtle and does not warrant taxonomic distinction at this point.

However, the results of these analyses deserve further consideration, as well. It has been demonstrated that approaches such as these frequently reflect the environmental component of the variation to be found among populations, while historical influences and genetically based variants are left undefined. More detailed analyses of cranial shape would give a better indication of what evolutionary units exist in this species (Smith and Patton 1980, 1988, Patton and Brylski 1987, Patton and Smith 1989). In a companion paper (Rogers 1991) I investigate the electrophoretic and karyotypic aspects of variation in *Thomomys townsendii* to supplement the results of this morphological study with information that is likely to be more representative of historical events and more informative about the phylogenetic history of the species (Smith and Patton 1980). The results of morphological and genetic analyses are then considered in the context of the biogeographic history of the northern Great Basin to present more clearly patterns of evolutionary differentiation of *Thomomys townsendii.*

ACKNOWLEDGMENTS

I thank J. L. Patton for his guidance and encouragement through all phases of this project and for the essential criticism he added to many drafts of this paper. D. B. Wake, W. Clemens, W. E. Bemis, B. D. Patterson, and W. T. Stanley provided helpful criticism and comments on this and earlier versions of the manuscript. Skeletal material was prepared by R. Jones. M. L. Johnson (Puget Sound Museum of Natural History, University of Puget Sound), D. J. Schmidly (Texas Cooperative Wildlife Collection, Texas A&M University), and B. J. Verts (Department of Fisheries and Wildlife, Oregon State University) provided specimens for analysis. C. Maser offered additional locality information. I am grateful to the ranchers and landowners who cooperated in my collecting efforts. For all their moral support I thank Owen and Hally Rogers. I thank W. E. Bemis, especially, for providing invaluable assistance in the field and consistent support throughout this project. This study and its companion paper are based on a thesis completed in partial fulfillment of requirements for the M.A. degree in the Department of Zoology, University of California, Berkeley. Financial support for this research was provided by the Department of Zoology, Museum of Vertebrate Zoology (two Louise M. Kellogg Grants-in-Aid), and National Science Foundation grant DEB 81-09677 to J. L. Patton. The Department of Anatomy, University of Chicago, and the Field Museum of Natural History generously provided use of their facilities.

LITERATURE CITED

Allison, I. S. 1966. Fossil Lake, Oregon. Its geology and fossil faunas. Oregon State Monographs, Studies in Geology 9: 1–48.

Bailey, V. 1915. Revision of the pocket gophers of the genus *Thomomys*. North American Fauna No. 39: 1–136.

Bowers, D. E. 1956. A study of methods of color determination. Systematic Zoology 5: 147–160, 182.

Cronquist, A., A. H. Holmgren, N. H. Holmgren, and J. L. Reveal. 1972. Intermountain Flora—Vascular plants of the Intermountain West, USA. Vol. 1. Hafner Publishing Co., New York. 270 pp.

Davis, W. B. 1937. Variations in Townsend pocket gophers. Journal of Mammalogy 18: 145–158.

______. 1938. Relation of size of pocket gophers to soil and altitude. Journal of Mammalogy 19: 338–342.

______. 1940. Distribution and variation of pocket gophers (genus *Geomys*) in the southwestern United States. Texas A & M College, Texas Agricultural Experiment Station Bulletin 590: 1–38.

Elftman, H. O. 1931. Pleistocene mammals of Fossil Lake, Oregon. American Museum Novitates 481: 1–21.

Gazin, C. L. 1935. Annotated list of Pleistocene Mammalia from American Falls, Idaho. Journal of the Washington Academy of Sciences 25: 297–302.

Genoways, H. 1973. Systematics and evolutionary relationships of spiny pocket mice, genus *Liomys*. Special Publications, The Museum, Texas Tech University, No. 5. 368 pp.

Grayson, D. K. 1982. Toward a history of Great Basin mammals during the past 15,000 years. Pages 82–101 *in* D. B. Madsen and J. F. O'Connell, eds., Man and environment in the Great Basin. Society for American Archaeology Papers, No. 2. Society for American Archaeology, Washington, D.C. vi + 242 pp.

Grinnell, J. 1927. Geography and evolution in the pocket gophers of California. Annual report of the Smithsonian Institution, 1926. Publication 2894: 343–355.

______. 1931. A new pocket gopher from southeastern California. University of California Publications in Zoology 38: 1–10.

______. 1935. Differentiation in pocket gophers of the *Thomomys bottae* group in northern California and southern Oregon. University of California Publications in Zoology 40: 403–415.

Gruhn, R. 1961. The archaeology of Wilson Butte Cave south-central Idaho. Occasional Papers of the Idaho State College Museum 6: 1–202.

Guilday, J. E. 1969. Small mammal remains from the Wasden Site (Owl Cave), Bonneville County, Idaho. Tebiwa 12: 47–57.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Vol. 1. The Ronald Press Company, New York. 546 pp.

Hay, O. P. 1921. Descriptions of species of Pleistocene Vertebrata, types or specimens of most of which are preserved in the United States National Museum. Proceedings of the United States National Museum 59 (2391): 599–642.

Hoffmeister, D. F. 1969. The species problem in the *Thomomys bottae–Thomomys umbrinus* complex of pocket gophers in Arizona. University of Kansas Museum of Natural History Miscellaneous Publications 51: 75–91.

Honeycutt, R. L., and D. J. Schmidly. 1979. Chromosomal and morphological variation in the Plains Pocket Gopher, *Geomys bursarius*, in Texas and adjacent states. Occasional Papers, The Museum, Texas Tech University 58: 1–54.

Hopkins, M. L., R. Bonnichsen, and D. Fortsch. 1969. The stratigraphic position and faunal associates of *Bison* (*Gigantobison*) *latifrons* in southeastern Idaho, a progress report. Tebiwa 12: 1–8.

Howard, W. E., and H. E. Childs, Jr. 1959. Ecology of pocket gophers with emphasis on *Thomomys bottae mewa*. Hilgardia 29: 277–358.

Ingles, L. G. 1950. Pigmental variations in populations of pocket gophers. Evolution 4: 353–357.

McDonald, H. G., and E. Anderson. 1975. A late Pleistocene vertebrate fauna from southeastern Idaho. Tebiwa 18: 19–37.

Merriam, C. H. 1895. Monographic revision of the pocket gophers family Geomyidae (exclusive of the species of *Thomomys*). North American Fauna 8: 1–258.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences. 2d ed. McGraw Hill Inc., New York. 675 pp.

Patton, J. L., and P. V. Brylski. 1987. Pocket gophers in alfalfa fields: causes and consequences of habitat-related body size variation. American Naturalist 130: 493–506.

Patton, J. L., J. C. Hafner, M. S. Hafner, and M. F. Smith. 1979. Hybrid zones in *Thomomys bottae* pocket gophers: genetic, phenetic, and ecologic concordance patterns. Evolution 33: 860–876.

Patton, J. L., and M. F. Smith. 1989. Population structure and the genetic and morphologic divergence among pocket gopher species (genus *Thomomys*). Pages 284–304 *in* D. Otte and J. Endler, eds., Speciation and its consequences. Sinauer Associates, Inc., Sunderland, Massachusetts.

Rogers, M. A. 1991. Evolutionary differentiation within the northern Great Basin pocket gopher, *Thomomys townsendii*. II. Genetic variation and biogeographic considerations. Great Basin Naturalist 51: 127–152.

Rohlf, F. J., J. Kishpaugh, and D. Kirk. 1980. NT-SYS. Numerical taxonomy system of multivariate statistical programs. Edited for use at the University of California, Berkeley, by T. Duncan, Department of Botany, University of California, Berkeley.

Selander, R. K., and R. F. Johnston. 1967. Evolution in the house sparrow. I. Intrapopulation variation in North America. Condor 69: 217–258.

Smith, M. F., and J. L. Patton. 1980. Relationships of pocket gopher (*Thomomys bottae*) populations of the lower Colorado River. Journal of Mammalogy 61: 681–696.

———. 1988. Subspecies of pocket gophers: causal bases for geographic differentiation in *Thomomys bottae*. Systematic Zoology 37: 163–178.

Smith, M. F., J. L. Patton, J. C. Hafner, and D. J. Hafner. 1983. *Thomomys bottae* pocket gophers of the central Rio Grande Valley, New Mexico: local differentiation, gene flow, and historical biogeography. Occasional Papers of The Museum of Southwestern Biology 2: 1–16.

Thaeler, C. S., Jr. 1968. An analysis of the distribution of pocket gopher species in northeastern California (Genus *Thomomys*). University of California Publications in Zoology 86: 1–46.

Yates, T. L., W. R. Barber, and D. M. Armstrong. 1987. Survey of North American collections of recent mammals. Journal of Mammalogy 68(2, suppl.): 1–76.

Received 16 January 1990
Revised 15 January 1991
Accepted 20 February 1991

APPENDIX

Specimens Examined

Listed below are specimens examined in the morphological and color analyses of this study. Boldface numbers preceding localities represent corresponding composite locality numbers. Each locality is followed by the sample size for the morphological analysis. Those specimens used in both the morphological and the color analyses are italicized, and specimens used only in the color analysis are italicized and marked with an asterisk (*). Museum acronyms follow Yates et al. (1987).

Thomomys townsendii nevadensis

CALIFORNIA: **Lassen Co., [30]**, Amedee (2 females): MVZ 77591, 77592; 4 mi. ESE Amedee (1 female): MVZ 77593; Honey L., 6 mi. NW Amedee, 4000 ft. (1 female): MVZ 32990; 3.4 mi. N, 2.6 mi. W Doyle, 4250± ft. (1 male): MVZ 124165; 3.7 mi. NNW Doyle, 4200 ft. (1 male): MVZ 163624; 1.8 mi. S, 1.6 mi. W Herlong, 4060 ft. (2 males): MVZ 124168, 124169; Garnier Ranch, 2.4 mi. S, 1.5 mi. W Herlong, 4130 ft. (15 males, 11 females): MVZ 130120–130127, 130129, 130131–130134, 130137, 130138, 130140, 130141, 138411–138415, 149985, 149988, 149994, 149995; 2.8 mi. W, 0.2 mi. S Herlong, 4030 ft. (1 female): MVZ 130156; Honey Lake Valley, Garnier Ranch, 3 mi. SW Herlong (3 males, 3 females): MVZ 138429–138434; 0.3 mi. S, 3.0 mi. W Herlong, 4030 ft. (1 female): MVZ 124166; Bird Flat Ranch, 3 mi. S, 2.7 mi. W Herlong, 4080 ft. (18 males, 9 females): MVZ 163597, *163598*, *163599*, 163600, *163601*, 163602, 163603, *163604*, 163605, *163606*, 163607–163623; 0.7 mi. S, 3.7 mi. W Herlong, 4020 ft. (1 male): MVZ 124167; 3.9 mi. W, 2.1 mi. S Herlong, 4030 ft. (6 males, 2 females): MVZ 130157–130164; Garnier Ranch, 5.0 mi. W, 1.5 mi. S Herlong, 4020 ft. (8 males, 5 females): MVZ 130143–130155; 5.1 mi. SW Herlong (by rd.) (4 males, 3 females): MVZ 149998, 150000, 150005, 150007, 150008, 150010, 150012; **[31]**, 3.0 mi. S Johnstonville, 4440 ft. (1 female): MVZ 126029; Elysian Valley, 5.0 mi. S, 0.1 mi. E Johnstonville, 4360± ft. (1 male): MVZ 126027; Elysian Valley, 5.3 mi. S, 0.3

mi. E Johnstonville, 4330 ft. (1 female): MVZ 126028; 3.4 mi. W, 3.3 mi. N Litchfield, 4140 ft. (1 male, 2 females): MVZ 126030, 126031, 126033; 4.2 mi. N, 3.4 mi. E Litchfield, 4160 ft. (1 female): MVZ 126529; 3.4 mi. W, 4.3 mi. N. Litchfield, 4160 ft. (1 female): MVZ 126034; 3.5 mi. N and 3.2 mi. W Milford, 4070 ft. (2 females): MVZ 126389, 126390; 0.2 mi. N, 0.2 mi. W Peter Lassen Grave, 4340 ft. (1 male, 2 females): MVZ 129038–129040; 0.7 mi. N, 0.2 mi. E Peter Lassen Grave, 4280 ft. (1 male): MVZ 129041; 0.4 mi. E Standish (1 female): MVZ 122150; 2.4 mi. W Standish (1 female): MVZ 122151; Zangger Ranch, 3.8 mi. W Standish (1 male, 3 females): MVZ 122154–122158; 4 mi. W Standish, 4110 ft. (2 males, 11 females): MVZ 163625–163628, *163629*, 163630, *163632*, *163633*, 163634, 163635, *163636*, *163637*, 163638; 5 mi. W Standish (1 male): MVZ 122153; 2 mi. S Susanville (1 male): MVZ 35271, *35273**; 3 mi. S Susanville, 4200 ft. (3 males): MVZ *63341*, *63342*, 63343; 3.1 mi. S Susanville, 4200 ft. (1 male, 1 female): MVZ 129252, *129253*; 4.5 mi. ENE Susanville, 4600 ft. (1 male, 2 females): MVZ 63335, 63337, *63338*; 1.0 mi. N, 0.3 mi. W Wendel, 4060 ± ft. (1 male): MVZ 126035; 1.1 mi. N, 1.4 mi. W Wendel, 4030 ± ft. (1 male): MVZ 126036; 1.1 mi. N, 3.2 mi. W Wendel, 4010 ± ft. (1 female): MVZ 126037; Honey Lake Refuge, 4 mi. W Wendel, 4000 ft. (1 female): MVZ 114490.

NEVADA: **Elko Co., [10]**, Elburz, 2 mi. W Halleck, 5200 ft. (1 male): MVZ *44442*; 11 mi. NE Elko, 5200 ft. (2 males, 1 female): TCWC *36156*, *36157**, *36158*, 36160; 4 mi. W Halleck, 5200 ft. (1 female): MVZ *67928*; 0.5 mi. SW Ryndon, 5100 ft. (10 males, 10 females): MVZ 163508–163514, *163515*, 163516–163518, *163519*, *163520*, 163521, 163522, *163523*, *163524*, 163525–163527; **[14]**, 24 mi. SE Wells, Independence Valley, 5900 ft. (1 female): MVZ 135337; **Eureka Co., [11]**, Evans (1 male, 1 female): MVZ 70583, *70584*; Hay Ranch, 17 mi. SE Palisade, 5160 ft. (3 males, 15 females): MVZ *163528*, 163529–163535, *163537*, *163538*, 163539–163541, *163542*, *163543*, 163544–163546; **[12]**, 4 mi. S Romano, Diamond Valley (3 females): MVZ 70587, *70588*, 70589; **[13]**, Winzell (1 male, 1 female): MVZ 70585, *70586*; **Humboldt Co., [2]**, 1 mi. E Golconda, 4000 ft. (2 females) and 4100 ft. (1 male): MVZ 94733, 94735, 94736; 18 mi. NE Iron Point, 4600 ft. (2 males, 1 female): MVZ 67924, *67925*, *67926*; 1 mi. N Winnemucca, 4600 ft. (3 males, 1 female): MVZ 67929, *67930*, 67932, *67933*; **[5]**, Big Creek Ranch, base of Pine Forest Mts., 4350 ft. (2 females): MVZ 7868, 7870; Quinn River Crossing, 4100 ft. (7 males, 12 females): MVZ 7854–7857, 7859, 7860, 7863, 7864, 7866, 7867, *163082*, *163083*, 163084, *163085*, *163086*, *163474*, *163475*, 163476, 163477; Jackson Creek Ranch, 17.5 mi. S and 5 mi. W Quinn River Crossing, 4000 ft. (1 male): MVZ 78655; **[6]**, 6 mi. E Division Peak, 4200 ft. (2 males, 2 females): MVZ 95297, *95298*, *95299*, *95300*; Flowing Sp., 7 mi. E and 3.5 mi. N Division Pk., 4200 ft. (1 male, 2 females): MVZ *95294*, 95295, 95296; **Lander Co., [15]**, Malloy Ranch, 5 mi. West of Austin, Reese River, 5500 ft. (12 males, 8 females): MVZ 37061, *37062*, 37063–37065, *37066*, 37067, *37068*, 37069–37072, 37074–37078, *37079*, *37080*, 37082; 5.5 mi. W Austin, 5700 ft. (5 males, 11 females): MVZ 163549, 163550, *163551*, 163552–163557, *163559*, *163560*, 163561, *163562*, *163563*, 163564, *163567*; **Pershing Co., [3]**, Lovelock, 3980 ft. (2 females): MVZ 64830, 64831; Big Meadow Ranch, Lovelock, 4000 ft. (3 males, 3 females): MVZ *163071**, *163072*, *163074*, *163075*, 163080, 163081, 163499; 3.3 mi. SW Lovelock (2 males, 2 females): MVZ 150014, 150016–150018; Toulon, 3930 ft. (1 female): MVZ 67934; **[1]**, 2 mi. NW Valmy, 4450 ft. (4 males, 17 females): MVZ *163478*, 163479, *163480*, 163481, 163482, *163483*, 163484, *163485*, 163486–163489, *163490*, 163491, *163492*, 163493, 163494, *163495*, 163496–163498; **[6]**, 11.5 mi. E and 22 mi. N Gerlach, 4200 ft. (1 male): MVZ 95301.

OREGON: **Harney Co., [4]**, 4 mi. SW Narrows, 4200 ft. (4 males, 1 female): MVZ 163502, 163504–163507; **[7]**, Lake Alvord, Alvord Desert (1 female): MVZ *44883*; S end Lake Alvord, 4300 ft. (2 males, 2 females): MVZ 78649–78651, *78652*; Borax Sprg., S end Lake Alvord, 4200 ft. (1 male): MVZ 78653; Alvord Valley, T37S, R33E, W 1/2 sec. 27 (1 male): PSM 20393; **[8]**, 20 mi. S, 10.1 mi. W Burns, 4200 ft. (1 female): OSUFW *2960*; 22.5 mi. S, 14.5 mi. E Burns (Malheur Refuge), (2 males, 3 females): OSUFW *1*, *2*, *3*, *4*, *5*; 26 mi. S, 7 mi. E Burns, 4200 ft. (1 female): OSUFW 2961; 28 mi. S, 3 mi. W Burns, 4100 ft. (1 male): OSUFW: *1646*; Malheur Environmental Field Station, between N and S Coyote Butte (1 female): PSM *24427*; 1 mile east of Malheur Refuge Headquarters (2 males): OSUFW *810*, *1933*; Narrows (5 mi. SW), 4000 ft. (2 males): MVZ 44885, 44886; **Malheur Co., [9]**, 3 mi. N McDermitt, Nevada (1 male): PSM *6108*.

Thomomys townsendii townsendii

IDAHO: **Bannock Co., [20]**, West Pocatello River bottom, Pocatello (1 male, 3 females): MVZ 46506, 46507, TCWC 494, 495; Pocatello Cr., 1 mi. NE Pocatello, 5000 ft. (3 males, 3 females): TCWC *33059**, 33061, *33062*, 33064–33067; 4 mi. NW Pocatello (4 males, 4 females): MVZ *46552*, 46553–46556, 46558–46560; Floyd Johnson Ranch, 4 mi. NW Pocatello, 4500 ft. (6 males, 7 females): MVZ 163639, 163640, 163642–163645, *163648**, 163650, 163651, *163652*, *163653*, *163654*, 163655, *163656*; Fort Hall Indian School, 10 mi. N Pocatello (1 male): MVZ *51904*; **Bingham Co., [20]** 1 mi. E Pingree MVZ *72020**, *72021**; **Canyon Co., [25]**, N side Snake River, 4 mi. S Wilder (1 male, 3 females): MVZ *72012*, 72013, *72014*, 72015; **Elmore Co., [22]**, 3 mi. E Grandview, 2800 ft. (3 females): MVZ 163671, 163672, *163673*; **[27]**, Hammett (5 males, 4 females): MVZ 72003–72006, *72007*, *72008*, 72009, 72010, *72011*; **Owyhee Co., [16]**, 7.5 mi. SE Grandview, 2600 ft. (7 males, 16 females): MVZ *163568*, 163569, *163570*, 163571, 163572, *163573*, 163574–163576, *163578*, *163579*, 163580–163589, 163591, 163592; **[17]**, 5 mi. SE Murphy (2 males, 2 females): MVZ *67495*, 67496–67498; 6 mi. SE Murphy, 3000 ft. (2 males, 1 female): MVZ 163593, *163595*, *163596*; Sinker Creek, 7 mi. SE Murphy (1 female): MVZ *67501*; Castle Creek, 8 mi. S Oreana (2 males, 3 females): MVZ *67489*, 67490, *67491*, 67492, *67494*; **[18]**, 1 mi. SE Bruneau, 2600 ft. (1 male, 2 females): TCWC *33055*, *33056*, 33058; Indian Cove (2 females): MVZ 72001–72002; **[26]**, S bank Snake River, Homedale (3 females): MVZ 71998–72000; **Payette Co., [23]**, 1.5 mi. NE Payette, 2200 ft. (5 males, 1 female): MVZ 163677–163679, *163680*, 163682, *163683*; 2 mi. S Payette between Payette and Snake Rivers (3 females): MVZ 67502, 67505, 67506; 3 mi. E Payette (4 males, 3 females): TCWC *25929*, 25930, 25931, *25933*, *25934*, 25935, 25936; **Power Co., [19]**, 2.5 mi. NW American Falls, 4500 ft. (7 females): MVZ 163658, 163660, 163662, *163664*, *163665*, 163666, *163667*; 4 mi. NW American Falls (1 female): MVZ 67507; **[21]**, 2.5 mi. SW Michaud, 4400 ft. (1 female): MVZ *51903*; 5.5 mi. SW Michaud, 4400 ft. (1 female): MVZ *51902*; **Washington Co., [23]**, 2.9 mi. SE Weiser, 2100 ft. (1 male): MVZ 163687.

OREGON: **Malheur Co., [29]**, Kane Springs (T21S, R43E, sec. 4) (2 females): PSM 20390, 20391; **[24]**, W side Snake River, Ontario (2 males): MVZ 72017, 72018; 2.5 mi. N Ontario, 2100 ft. (2 males, 7 females): MVZ 163691, 163694–163696, 163701, 163702, *163704*, 163706, 163707; **[28]**, 1 mi. N, 5 mi. E Vale, 2500 ft. (1 male): OSUFW *3490*; 2 mi. N Vale (1 female): PSM *19109*; 3.5 mi. S Vale, 2270 ft. (6 males, 2 females): PSM 20382–20389; 5 mi. S, 2 mi. W Vale, 2300 ft. (1 male): OSUFW *2695*; 6.5 mi. SSE Vale, 2799 ft. (1 male, 1 female): PSM *20380*, *20381*.

Great Basin Naturalist 51(2), 1991, pp. 127–152

EVOLUTIONARY DIFFERENTIATION WITHIN THE NORTHERN GREAT BASIN POCKET GOPHER, *THOMOMYS TOWNSENDII*.

II. GENETIC VARIATION AND BIOGEOGRAPHIC CONSIDERATIONS

Mary Anne Rogers[1]

ABSTRACT.—Genetic variation across the known geographic range of *Thomomys townsendii* was examined by starch gel electrophoresis and nondifferentially stained karyotypes. All specimens examined had a diploid number of 76, but some populations possessed one pair of acrocentric chromosomes in an otherwise biarmed karyotype. Electrophoretic analyses of 16 populations revealed *Thomomys townsendii* to be among the least variable of pocket gopher species studied. Of 27 loci examined, 17 were monomorphic and heterozygosity values were low (H = .000-.028, $\bar{H}$ = .012). Genic differentiation between populations was also low (S = .896-.998, $\bar{S}$ = .956) and revealed little concordance with current subspecific units. The most marked differentiation is between the Honey Lake Valley/Humboldt River region and the Snake River drainage. Within each of these regions population variation is, in some cases, greater within than between currently defined subspecies. F-statistics show that the greatest genic differentiation is seen between populations, and a comparison of subspecies within a region shows the greatest homogeneity. The evolutionary history of *Thomomys townsendii* is discussed in the context of both the physiographic history of the region and the affinities of this species to *Thomomys bottae*. Results of this study and the patterns of differentiation found in the morphological analyses of the accompanying paper (Rogers 1991) indicate that the only consistent pattern to be discerned from the overall morphological and genetic homogeneity of *Thomomys townsendii* is that between populations of the Humboldt and Snake River drainage systems, which are here assigned to *Thomomys townsendii nevadensis* and *Thomomys townsendii townsendii*, respectively.

Key words: Thomomys townsendii, *pocket gophers, genetic variation, evolutionary differentiation, geographic variation, electrophoresis, karyotype.*

Since the revisions by Merriam (1895) and Bailey (1915), many studies have focused on defining and understanding morphological variation within the family Geomyidae. Aspects of fossoriality, such as specificity to soil type and low vagility, and environmental influences, such as climate, topography, and food resources, have long been considered in this context (Bailey 1915, Grinnell 1927, Davis 1937, 1940, Hall 1946, Ingles 1950). More recently, patterns of chromosomal and electrophoretic variation have been compared to and correlated with interrelationships among habitat preference, physiographic features, gene flow, and population size (Patton 1970, 1972, 1981, Nevo et al. 1974, Penney and Zimmerman 1976, Patton and Yang 1977, Honeycutt and Schmidly 1979, Tucker and Schmidly 1981, Sudman et al. 1987). To explain the patterns found, investigators have presented different arguments for a variety of evolutionary mechanisms. Patterns of genetic variation in pocket gophers have been attributed to the selective forces associated with the homogeneous fossorial environment (Nevo et al. 1974, Penney and Zimmerman 1976) or to a series of stochastic processes and physiographic changes (Patton 1972, 1981, Patton and Yang 1977).

The geographic distribution and phylogenetic affinities of *Thomomys townsendii* make this species an interesting subject for genetic analyses. The presence of *T. townsendii* in the northern Great Basin is influenced by the distribution of deep fluviatile and lacustrine soils and by the physical and biological barriers that interrupt and restrict these habitats. Patton and Smith (1981) examined allozymic and karyotypic relationships within the *bottae* group and determined *T. townsendii* to be derived from one of the geographic units of *T. bottae*. This genetic evidence and the morphological similarity found between these two species (Patton and Smith 1989) provide an evolutionary framework within which to interpret the patterns

---

[1] Department of Zoology, Field Museum of Natural History, Chicago, Illinois 60605.

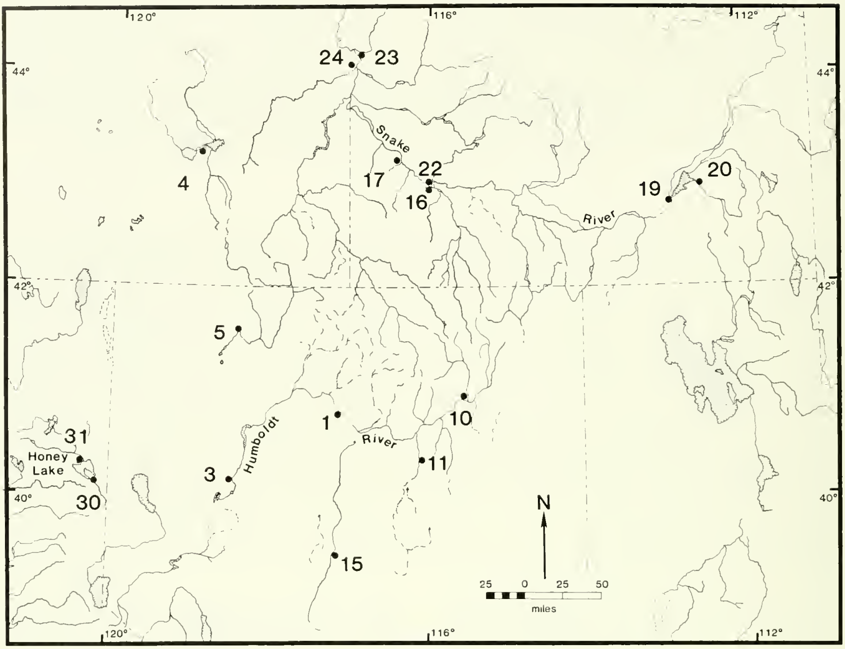


Fig. 1. Map of localities sampled for electrophoretic and karyotypic analyses. Locality information is given in the Appendix.

of allozymic and karyotypic variation of *T. townsendii.* Given the apparent phylogenetic affiliation, results of genetic analyses of *Thomomys bottae* synthesized by Patton (1981) are especially relevant to the present examination of genetic differentiation within *Thomomys townsendii.* In general, genic patterns in *T. bottae* do not reflect subspecific, topographic, or vegetational boundaries. Instead, broader geographic units are defined both karyotypically and genically. This pattern suggests that environmental factors often do not explain patterns of genetic variation, but historical biogeography and features of gopher populations such as vagility and effective population size may be influential.

The results of the genetic analyses of this study and the patterns of morphological variation discussed in the accompanying paper (Roger 1991) will be considered in the context of the biogeographic history of the region and the phylogenetic affinities of this species. These components of the biology of *Thomomys townsendii* make it possible to assess its evolutionary differentiation and the validity of current taxonomic designations of this species.

Materials and Methods

Electrophoretic Procedures

During the spring and summer of 1981 and the spring of 1982, 252 gophers were collected using Macabee gopher traps. Sixteen populations from areas representing all seven recognized subspecies and the entire geographic range of *Thomomys townsendii* were sampled. The localities (numbered as in the accompanying morphological study [Rogers 1991]) and sample sizes are detailed in Figure 1 and in the Appendix.

These animals were preserved as skin and skull, skeleton only, or skull only specimens and are deposited in the Museum of

Vertebrate Zoology, University of California, Berkeley. Kidney, liver, and hemolysate and plasma blood fraction samples were prepared and then frozen in liquid nitrogen. Samples were later stored under ultra-cold conditions (−76 C) in the laboratory. Kidney and liver samples were homogenized in grinding buffer and centrifuged to produce extracts. Extracts and plasma samples were then analyzed by horizontal starch gel electrophoresis following procedures similar to Selander et al. (1971). The 27 loci scored and the tissue types used (K = kidney, L = liver, P = plasma) are as follows: *enzymatic proteins:* aconitase (E.C. 4.2.1.3, ACON; K), adenosine deaminase (E.C. 3.5.4.4, ADA; K), α-glycerophosphate dehydrogenase (E.C. 1.1.1.8, αGPD; K), alcohol dehydrogenase (E.C. 1.1.1.1, ADH-2; L), esterase (E.C. 3.1.1.1, EST-4; K), glucosephosphate isomerase (E.C. 5.3.1.9, GPI; K), glutamate-oxaloacetate transaminase (E.C. 2.6.1.1, GOT-1, GOT-2; K), glyceraldehyde phosphate dehydrogenase (E.C. 1.2.1.12, GAPDH; K), isocitrate dehydrogenase (E.C. 1.1.1.42, ICD-1, ICD-2; K), lactate dehydrogenase (E.C. 1.1.1.27, LDH-1, LDH-2; K), leucine aminopeptidase (E.C. 3.4.11 or 3.4.13, LAP; K), malate dehydrogenase (E.C. 1.1.1.37, MDH-1, MDH-2; K), mannose phosphate isomerase (E.C. 5.3.1.8, MPI; K), peptidase (leucyl-alanine substrate, E.C. 3.4.11 or 3.4.13, PEP-C; K), peptidase (leucyl-glycyl-glycine substrate, E.C. 3.4.11 or 3.4.13, PEP-B; K), phosphoglucomutase (E.C. 2.7.5.1, PGM-2; K), phosphogluconate dehydrogenase (E.C. 1.1.1.44, 6 PGD; K), purine nucleoside phosphorylase (E.C. 2.4.2.1, NP; K), sorbitol dehydrogenase (E.C. 1.1.1.14, SORDH; K), superoxide dismutase (E.C. 1.15.1.1, SOD; K); *nonenzymatic proteins:* albumin (ALB; K), prealbumin (PREALB; P), transferrin (TRF; P).

Karyotypic Procedures

Forty-one animals, representing all recognized subspecies of *Thomomys townsendii* (Appendix), were examined. Most were pretreated with yeast (Lee and Elder 1980, with modifications in dosage). Chromosome preparations were made from bone marrow cells as described by Patton (1967) except that KCl was used as the hypotonic solution. Air-dried slides were stained in Giemsa (10% stock stain solution in phosphate buffer) and air-dried before mounting with coverslips. Determination of diploid numbers and construction of karyotypes followed standard procedures (Bender and Chu 1963, Patton 1967). Bi-armed chromosomes were categorized into either a metacentric/submetacentric class or a subtelocentric class after Patton and Dingman (1970), utilizing the arm ratio criteria of Patton (1967).

Statistical Analyses: Electrophoretic Data

Alleles were designated alphabetically in order of increasing mobility, and genotype frequencies were analyzed using the BIOSYS-1 computer program (Swofford and Selander 1981). Analyses of geographic differentiation utilized Wright's (1978) *F*-statistics, and trees were constructed from coefficients of genetic similarity and genetic distance (Rogers' *S*, *D* [1972] and modified *D* [Wright 1978]) using UPGMA clustering and the distance Wagner method (Farris 1972).

RESULTS

Intrapopulation Variation

Seventeen of the 27 loci examined were monomorphic. All polymorphic loci are represented by dominant alleles with frequencies of 0.95 or less with the exception of GOT-1 (Table 1). This locus is fixed for alternate alleles in the populations of Honey Lake Valley and the Humboldt River drainage system versus those of the Snake River system. Using the 0.95 criterion of polymorphism, only EST-4 is polymorphic in more than 3 of the 16 populations studied.

Intrapopulation variation is also low across loci. Population averages for *H* (mean proportion of loci heterozygous per individual, direct count estimate), *P* (proportion of loci polymorphic, 0.95 criterion), and *A* (mean number of alleles per locus) are presented in Table 1. The mean number of alleles per locus per population ranges from 1.0 to 1.11, with a mean across populations of 1.07. The proportion of the loci that is polymorphic per population ranges from .000 to .111. Mean polymorphism, *P*, calculated across the *T. townsendii* populations studied, is .053. Heterozygosity values range from .000 in Murphy ($n = 4$) and .002 in Pocatello ($n = 19$) to .028 in Grandview-*t*. ($n = 8$). The average

Table 1. Allele frequencies for polymorphic loci, and values for *H*, *P*, and *A*.

		Lovelock	Valmy	Quinn River Crossing	Narrows	Ryndon	Palisade	Austin	Herlong	Standish	American Falls	Pocatello	Grandview-*o*.	Murphy	Grandview-*t*.	Payette	Ontario
Population No.		3	1	5	4	10	11	15	30	31	19	20	16	17	22	23	24
(*n*)		(16)	(21)	(9)	(6)	(20)	(19)	(22)	(27)	(18)	(10)	(19)	(21)	(4)	(8)	(12)	(20)
Locus/Allele																	
GOT-1	a	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000							
	b										1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM	a	.625															
	b	.375	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.375	1.000	1.000
	c														.625		
ADH	a								.370	.111							
	b	1.000	1.000	1.000	.250	1.000	1.000	1.000	.630	.889	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	c				.750												
EST-4	a						.184	.023	.019	.028	.050	.132	.190			.250	.075
	b	1.000	.929	1.000	1.000	1.000	.816	.977	.981	.972	.950	.868	.810	1.000	1.000	.750	.925
	c		.071														
GAPDH	a		.048														
	b		.048														
	c	1.000	.904	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PREALB	a	1.000	1.000	1.000	1.000	.800	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	b					.200		1.000									

TABLE 1 continued.

TRF	a						.026								.125		
	b	1.000	1.000	1.000	1.000	1.000	.974	1.000	1.000	1.000	1.000	1.000	.905	1.000	.875	1.000	1.000
	c												.095				
ADA	a					.275											
	b						.053	.023									
	c	1.000	1.000	1.000	1.000	.725	.947	.977	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.950
	d																.050
MPI	a			.167													
	b	1.000	1.000	.833	1.000	1.000	.947	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	c						.053										
PEP-B	a															.167	.050
	b	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.833	.950
H		.014	.009	.012	.019	.031	.016	.003	.018	.006	.004	.002	.007	.000	.028	.019	.009
P		.037	.074	.037	.037	.074	.111	.000	.037	.037	.037	.037	.074	.000	.074	.074	.111
A		1.04	1.11	1.04	1.04	1.07	1.15	1.07	1.07	1.07	1.04	1.04	1.07	1.00	1.07	1.07	1.11

TABLE 2. Matrix of between-population genetic similarity using Rogers' *S* (1972).

Population	3	1	5	4	10	11	15	30	31	19	20	16	17	22	23	24
3 Lovelock	—															
1 Valmy	.971	—														
5 Quinn River	.971	.988	—													
4 Narrows	.949	.967	.966	—												
10 Ryndon	.959	.977	.976	.955	—											
11 Palisade	.965	.986	.985	.961	.973	—										
15 Austin	.938	.957	.955	.934	.960	.953	—									
30 Herlong	.962	.981	.979	.975	.968	.975	.948	—								
31 Standish	.972	.991	.989	.973	.977	.985	.958	.990	—							
19 Amer. Falls	.938	.958	.955	.933	.944	.953	.924	.948	.958	—						
20 Pocatello	.935	.956	.952	.930	.940	.956	.921	.945	.955	.997	—					
16 Grandview-*o.*	.929	.950	.946	.925	.935	.956	.915	.939	.949	.991	.994	—				
17 Murphy	.940	.957	.957	.935	.945	.951	.924	.949	.958	.998	.995	.989	—			
22 Grandview-*t.*	.935	.929	.929	.907	.918	.925	.896	.921	.930	.970	.967	.966	.972	—		
23 Payette	.924	.945	.941	.920	.930	.949	.910	.934	.944	.986	.989	.988	.985	.957	—	
24 Ontario	.933	.953	.950	.929	.942	.952	.921	.943	.953	.995	.994	.988	.994	.966	.987	—
	3	1	5	4	10	11	15	30	31	19	20	16	17	22	23	24

TABLE 3. Rogers' *S* (1972) coefficient of similarity averaged by subspecies and by region.

Subspecies	# pops.	1	2	3	4	5	6	7
1 *bachmani*	4	.969						
2 *elkoensis*	2	.970	.973					
3 *nevadensis*	1	.946	.956	****				
4 *relictus*	2	.978	.976	.953	.990			
5 *similis*	2	.945	.948	.923	.952	.997		
6 *owyhensis*	2	.942	.947	.920	.949	.995	.989	
7 *townsendii*	3	.933	.936	.909	.938	.984	.982	.970
Region	# pops.	1	2	3				
1 Humboldt River	7	.964						
2 Honey Lake	2	.974	.990					
3 Snake River	7	.937	.945	.984				

****Only one population included.

heterozygosity was calculated across the 12 populations of $n \geq 10$. The value for $\bar{H}$ was not altered ($\bar{H} = .012$).

Interpopulation Differentiation: Electrophoretic Analysis

The populations of *T. townsendii* examined were arranged within four hierarchical levels: local population, subspecies, region, and species. The geographic regions (and corresponding subspecies) included the following: the Humboldt River drainage system (*T. t. bachmani, T. t. elkoensis, T. t. nevadensis*), Honey Lake Valley (*T. t. relictus*), and the Snake River drainage system (*T. t. owyhensis, T. t. similis, T. t. townsendii*). Tables 2 and 3 represent the matrices of genetic similarity based on Rogers' *S* (1972) for the 16 populations, 7 subspecies, and 3 regions examined.

The range in similarity values for the populations of *T. townsendii* is .896 to .998, with $\bar{S} = .956$. Examination of the subspecific and regional treatments of these data reveals some discordance between subspecific or regional affinity and degree of genetic similarity. For example, in Tables 2 and 3 some populations of *T. t. bachmani* exhibit, on average, more genetic similarity to *T. t. elkoensis* and *T. t. relictus* than to other members of their own subspecies. These results are similarly displayed in the regional comparison where some populations of the Humboldt River region show a higher average similarity to Honey Lake than to some of the other populations within the Humboldt River system.

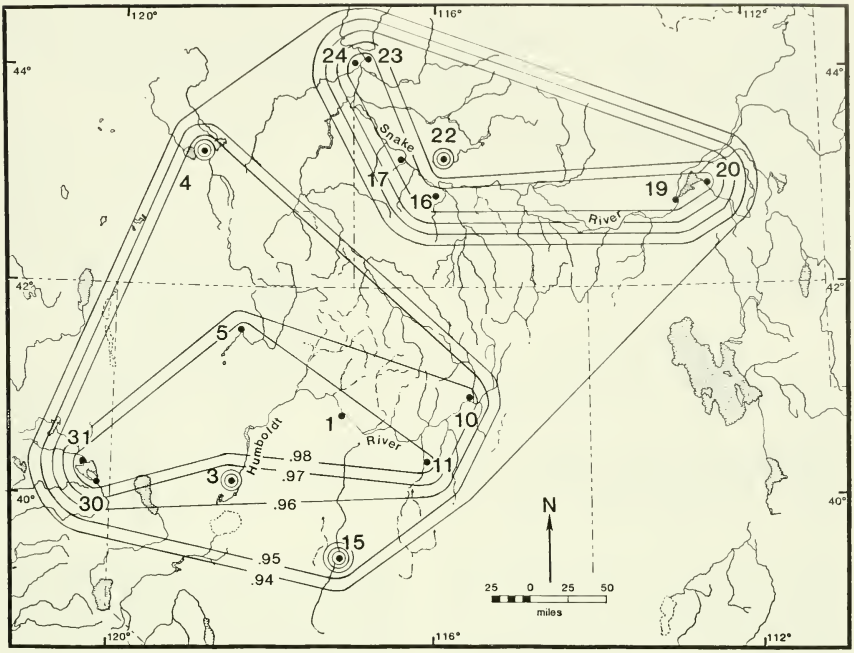


Fig. 2. Contour diagram derived from UPGMA phenogram based on Rogers' (1972) coefficient of similarity, S. Intervals represent a Rogers' S of .01. Goodness-of-fit statistics for phenogram are as follows: Farris (1972) F = 0.977, Prager and Wilson (1976) F = 0.852, percent standard deviation of Fitch and Margoliash (1967) = 1.187, cophenetic correlation coefficient = 0.882.

The Snake River subspecies are, however, on average most similar to the other subspecies of that region.

The unweighted pair group method of analysis was employed to cluster these data and illustrate these same trends in interpopulation similarities. Figure 2 presents the results of this analysis in the form of a contour diagram. Beyond general homogeneity among the *T. townsendii* populations (S = .939), the most obvious feature of the contour diagram is the separation of the Honey Lake Valley and Humboldt River populations from the Snake River populations, forming two major clusters ($S > .95$). This dichotomy is concordant with subspecific designations and hydrographic relationships. Within each cluster, however, similarity values do not correspond to current taxonomy or geographic affinities. For instance, within the Humboldt River/Honey Lake cluster, the populations of geographically peripheral *T. t. relictus* (Standish and Herlong) show affinities to some of the populations of the Humboldt River subspecies. The Standish population from Honey Lake Valley and the Valmy population from north central Nevada are the most similar pair of that major cluster and are therefore more similar to each other than either is to any other representative of its own subspecies. The *T. t. nevadensis* sample from Austin is the most divergent population from the Humboldt River region. Within the Snake River cluster, the greatest genic similarity values are also found between geographically well-separated populations. Grandview-*t.*, a *T. t. townsendii* population situated centrally in the Snake River distribution, is the most differentiated population of that cluster.

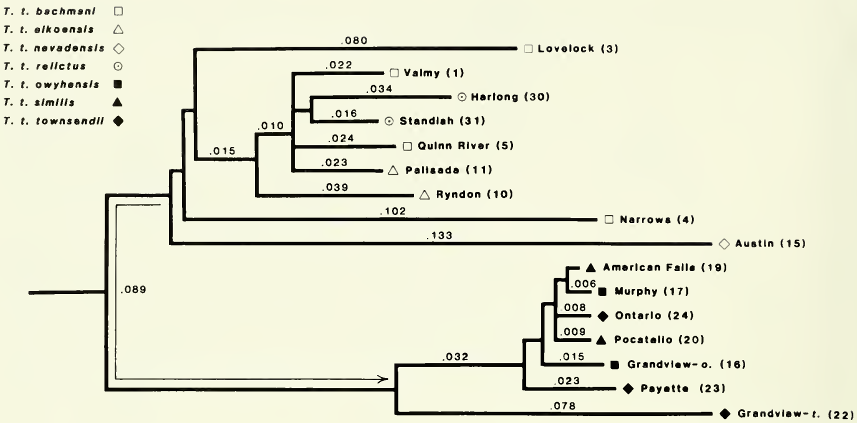

T. t. bachmani □
T. t. elkoensis △
T. t. nevadensis ◇
T. t. relictus ⊙
T. t. owyhensis ■
T. t. similis ▲
T. t. townsendii ◆
.080
□ Lovelock (3)
.022
□ Valmy (1)
.034
⊙ Harlong (30)
.016
⊙ Standish (31)
.010
.024
□ Quinn River (5)
.015
.023
△ Palisade (11)
.039
△ Ryndon (10)
.102
□ Narrows (4)
.133
◇ Austin (15)
▲ American Falls (19)
.006
■ Murphy (17)
.089
.008
◆ Ontario (24)
.009
▲ Pocatello (20)
.032
.015
■ Grandview-o. (16)
.023
◆ Payette (23)
.078
◆ Grandview-t. (22)

Fig. 3. Wagner tree based on Wright's (1978) modification of Rogers' *D*. Tree is rooted at midpoint and was constructed using Swofford's (1981) optimization algorithm. Goodness-of-fit statistics for tree are as follows: Farris (1972) F = 0.631, Prager and Wilson (1976) F = 3.255, percent standard deviation of Fitch and Margoliash (1967) = 9.358, cophenetic correlation coefficient = 0.995.

Figure 3 provides a phylogenetic tree produced by the distance Wagner procedure of Farris (1972) based on Wright's (1978) modification of Rogers' *D*. Additional trees, constructed with and without the use of Swofford's (1981) optimization algorithm and using Rogers' *D* (1972), give the same general topology. The most notable difference among these trees is in the position of the divergent populations within the Humboldt River cluster. Trees generated using Rogers' *D* (1972) show these populations arising from within different small clusters (all separated from adjacent clusters by branch lengths less than .01), in contrast to their peripheral position in trees generated with the modified Rogers' *D* (Wright 1978). Of the four trees generated, the one presented in Figure 3 was chosen for its high correlation coefficient (range in cophenetic correlation coefficients = .986–.995).

Several features are shared by the contour diagram derived from the UPGMA phenogram and all four Wagner trees. The most notable is the existence of two major clusters that separate the populations into the two river drainage systems. Divergent populations within each of these clusters are consistently well differentiated in all the algorithm/coefficient combinations utilized. These populations are Austin, Narrows, Lovelock, and Grandview-*t*. Each main cluster consists of a group of populations that cluster at a relatively high level of similarity and whose identity as a group is maintained in all analyses. Beyond the basic dichotomy between the two major river systems, there is no apparent concordance between geographic distance or hydrographic relationship and genic similarity.

The *F*-statistics of Wright (1978) were calculated to assess how genetic differentiation is partitioned within and between the hierarchical levels established in this study. As mentioned above, the 16 populations sampled correspond to the lowest level of the hierarchy, with subspecies, regions, and the total as higher levels. The variance components and F_{ST} values estimating the amount of variation accounted for by each of the subdivisions relative to another are given in Table 4. These were calculated for the polymorphic loci only. The greatest amount of differentiation is seen in comparing all the populations sampled (F_{ST} = .672). Of the comparisons made, subspecies compared within a region are the least differentiated (F_{ST} = .151). Within the total, interpopulation comparisons show greater differentiation than those between subspecies; these in turn show greater genic divergence than do comparisons between regions.

TABLE 4. Variance components and F-statistics (Wright 1978) combined across polymorphic loci.

Comparison	Variance component	F_{ST}
Three geographic regions used in hierarchical classification (Humboldt River, Honey Lake Valley, Snake River)		
Population–subspecies	.252	.392
Population–region	.366	.484
Population–total	.798	.672
Subspecies–region	.114	.151
Subspecies–total	.547	.460
Region–total	.433	.364
Two geographic regions used in hierarchical classification (Humboldt River/Honey Lake Valley and Snake River)		
Population–subspecies	.252	.392
Population–region	.342	.468
Population–total	.798	.672
Subspecies–region	.091	.124
Subspecies–total	.574	.460
Region–total	.456	.384

Similarly, within a region, interpopulation differentiation is greater than that measured between subspecies. Averaged across all loci, the F_{ST} calculated for all populations is .130.

The same statistics were calculated for a classification scheme with two regions, Honey Lake Valley populations being included with those of the Humboldt River drainage (Table 4). This set of F-statistics shows decreased differentiation between the populational and subspecific units within a region and greater differentiation between regions compared to the results of the three-region scheme. Honey Lake Valley populations fit relatively homogeneously into the Humboldt River region. The overall pattern still suggests that the greatest extent of differentiation is between the smallest subdivisions and that there is relative homogeneity between the subspecies of a region.

The total limiting variance or total gene diversity (HT of Nei 1973, 1977) per locus was calculated for each of the 10 polymorphic loci. GOT-1 exhibits the highest level of diversity, reflecting the fixed difference between the Humboldt/Honey Lake region and the Snake River region ($HT = .492$). This locus is probably responsible for most of the homogeneity (low F_{ST}) found among subspecies within a region. Four polymorphic loci have moderate HT values (.120-.147) while the five remaining polymorphic loci are low (.012-.049). Locus-by-locus chi square tests for heterogeneity between populations were also calculated. Those loci that exhibit the most significant levels of heterogeneity (GOT-1, PGM-1, ADH-2, and PREALB) are, for the most part, the same loci that create the greatest differentiation between the various hierarchical levels in the F-statistic analysis. These loci also contribute to the level of differentiation seen in the four divergent populations, Austin, Narrows, Lovelock, and Grandview-*t*.

Interpopulation Variation: Karyotypic Analysis

All individuals karyotyped showed a diploid number of 76. Five of the seven subspecies (*T. t. elkoensis*, *T. t. nevadensis*, *T. t. owyhensis*, *T. t. similis*, and *T. t. townsendii*) are represented by 16 pairs of meta- or submetacentric chromosomes ranging in size from large to small, and 21 pairs of large to small subtelocentric chromosomes (fundamental number [FN] = 148). In contrast, *T. t. bachmani* and *T. t. relictus* are characterized by 16 pairs of meta- or submetacentrics, 20 pairs of subtelocentrics, and a single medium-sized acrocentric pair (FN = 146). All seven subspecies have a large submetacentric X chromosome and a minute acrocentric (dot) Y chromosome.

PHYSIOGRAPHIC HISTORY OF THE NORTHERN GREAT BASIN

The Great Basin extends from the Sierra Nevada and Cascade Range in the west to the Wasatch Range and Colorado Plateau in the east. The northern and southern limits are defined by the Columbia and Colorado plateaus and the Mojave and Sonoran deserts. The Great Basin has internal drainage and is made up of over 150 smaller basins, separated by more than 160 north-south–oriented mountain ranges (Morrison 1965). Many of the rivers, lakes, and playas of these basins are remnants of the Pleistocene lakes Bonneville and Lahontan.

The climate of the Great Basin is semiarid to arid. Mean annual precipitation varies from year to year and increases with elevation. Precipitation may range from 10 cm in the basins

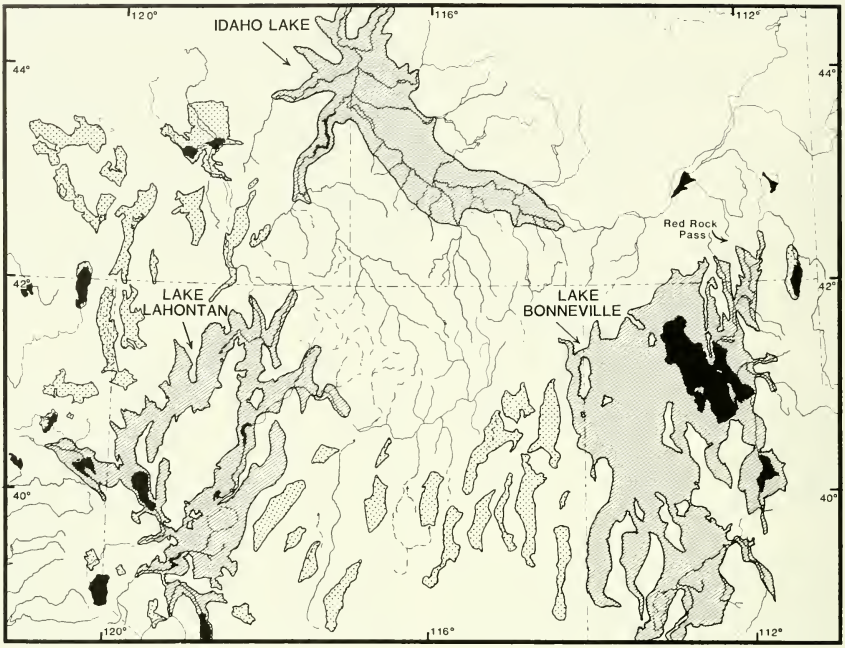


Fig. 4. Map of late Pliocene and Pleistocene lakes of the northern Great Basin (after Morrison 1965 and Wheeler and Cook 1954). The limits of Idaho Lake, Lake Lahontan, and Lake Bonneville are indicated by diagonal shading. Idaho Lake is of late Pliocene/early Pleistocene age. Lakes Lahontan and Bonneville and smaller lakes (stippled) are of Pleistocene age. Present-day lakes are represented by solid black areas. Point of overflow of Lake Bonneville at Red Rock Pass is indicated by arrow.

to over 76 cm in some of the higher mountains. Average January temperatures range from 25 F (−4 C) at Burns, Oregon, to 44.5 F (7 C) at Las Vegas, Nevada. Average July temperatures range from 67 F (19 C) at Burns to 86 F (30 F) at Las Vegas (Morrison 1965). As there are no drainages from the basin, precipitation is lost only to evaporation and transpiration. Evaporation increases and precipitation decreases in a southward trend. This latitudinal trend, coupled with the effect of elevation on temperature and evaporation, influences hydrographic features of the present-day Great Basin, as well as the existence and size of Pleistocene lakes (Meinzer 1922, Mifflin and Wheat 1979).

Pleistocene Lake Lahonton

The Great Basin of the Quarternary was divided, as today, into many hydrographic basins, the two largest of which were Lake Lahontan and Lake Bonneville (Fig. 4). Only the features of Lake Lahontan will be emphasized here, as the area covered by this drainage is closely reflected by the range of *Thomomys townsendii* in the northern Great Basin. Details of the features of Lakes Lahontan and Bonneville can be found in the monographs of Russell (1885) and Gilbert (1890). Broecker and Kaufman (1965), Morrison (1965), and Benson (1978) provide more recent discussions of the history of these basins.

The present-day Lahontan drainage includes parts of eastern California, southeastern Oregon, and much of northern Nevada. To the west and south it includes the Eagle Lake, Honey Lake, Lake Tahoe, and Walker Lake systems. The Reese and Humboldt rivers drain into Lahontan Basin from the east and south while the Quinn River makes up the northern component. The boundaries of the lake, at its highest level during the Wisconsin, encompassed the following drainage basins: Honey Lake, Pyramid Lake, Winnemucca Lake, Carson Lake, Walker Lake, Smoke Creek Desert, Black Rock Desert, part of the Truckee River, Humboldt River (eastward to a point near Golconda), and Quinn River (Russell 1885, Benson 1978).

The climate of the Wisconsin was characterized by great fluctuations in temperature and precipitation. Cool, wet times (pluvials), synchronous with the glacial intervals, resulted in high water levels in the Great Basin lakes. Each lacustral maximum was followed by warmer, drier periods during which the lakes subsided. A variety of interpretations exists for the extent and timing of the fluctuation of the level of Lake Lahontan (Broecker and Kaufman 1965, Morrison 1965, Benson 1978). Benson (1978) suggests that besides the most recent pluvial episode (spanning roughly 25,000 to 9,000 years before present [YBP]) Lake Lahontan reached at least one other high stage before 40,000 YBP. He found no evidence for high lake levels between 40,000 and 25,000 YBP but recognized two subsequent to that time: 25,000–21,500 YBP and 13,600–11,000 YBP. The intervening period represented lower lake levels, but most basins remained connected during this time.

Subsequent to the second deep-lake period, the climate of the Great Basin began a warming and drying trend (Antevs 1948). From 9000 to 5000 YBP the Lahontan Basin was warm and arid, with all lakes except Pyramid Lake desiccated. In the last 5000 years water levels rose in Pyramid and Walker lakes until they were tapped for agricultural use during the past 100 years (Benson 1978).

The pre-Wisconsin history of the Great Basin is not as well documented as that of Lake Lahontan time. Since lakes of the early and mid-Quaternary probably occupied regions that lakes Lahontan and Bonneville occupied subsequently, the majority of these deposits have been buried by younger ones. Exposed deposits, however, suggest two pre-Wisconsin lacustral intervals correlated with the Kansan and Illinoian glaciations. Early deposits from outside the areas inundated by Lake Lahontan have been found in the following regions: along the middle Reese River, Pine Valley, Smith Valley, and Carson Valley (Morrison 1965).

Snake River Plain

While the Snake River Plain is hydrographically not part of the Great Basin, it is a natural component in terms of fauna, flora, and climate (Davis 1939, Cronquist et al. 1972). As much of the northern part of the distribution of *T. townsendii* lies within this area, the physiographic history of the Snake River is pertinent to this study.

The Snake River Plain has been shaped by a long history of lava flows. The geography of the eastern plain is more dominated by remnants of volcanic activity than is the west. These eastern lavas are, in general, younger (late Pleistocene to Recent) than those of the western basin. Kuntz et al. (1986) suggest a minimum age range of 15,000–2,000 YBP for some of these formations. Pleistocene lavas forced the Snake River into its present course along the east plain and formed the surface of the plain there (Malde 1965).

The topographically diverse western plain is cut by more tributaries and canyons of the Snake River and is covered with lacustrine and fluviatile deposits. Some of the western lacustrine deposits can perhaps be explained by the former route of the Snake River and the establishment of Idaho Lake (Fig. 4). Wheeler and Cook (1954) suggest a possible late Pliocene route to the Pacific, running from western Idaho to southern Oregon via the Owyhee River. The route continues southwestward along the Steens, Pueblo, and Pine Forest mountains, across Black Rock and Smoke Creek deserts of Nevada to Honey Lake Valley. From here it moves to Chilcoot Pass and westward to the Feather River. In the late Pliocene/early Pleistocene the waters of the Snake were impounded and Idaho Lake formed in western Idaho and eastern Oregon. In early Pleistocene times Idaho Lake found an outlet, and the Snake River began its northward course into the Columbia drainage. Alternatively, Taylor (1960) suggests that the early route of the Snake River may have emptied into the Pacific via the Klamath River rather than the Feather River.

Another hydrographic link within the northern Great Basin is seen in the incidence of overflow of Lake Bonneville into the Snake River Plain. The Bonneville basin experienced a Wisconsin pluvial history similar to that described for Lake Lahontan. During one of the deep-lake periods, Lake Bonneville overflowed at Red Rock Pass (SE of Pocatello, Idaho; Fig. 4) into a tributary of the Snake River (Morrison 1965). Malde (1968) discusses the details of the catastrophic flood and the confusion over the age of the event. It is here regarded as late Wisconsin, about 12,000 YBP (Broecker and Kaufman 1965, Morrison 1965). The flood path extended across the Snake River Plain and parts of the bed of ancient Idaho Lake to a point only several miles from the Oregon border. The duration of major flood effects is estimated at a few days, although discharge continued for at least a year.

Historical Biogeography of *Thomomys townsendii*

Today *Thomomys townsendii* is found in fluviatile and lacustrine soils of southern Oregon and Idaho, northern Nevada, and northeastern California (Rogers 1991: Fig. 1). At the western edge of its distribution, *townsendii* is found in the Honey Lake Valley. To the northeast the species inhabits the Quinn River drainage system, Black Rock Desert, Alvord Desert, and the basin of Harney and Malheur lakes. Gophers follow the Humboldt River from Lovelock to the vicinity of Wells, Nevada. They are distributed along the Little Humboldt River and other tributaries to the north of the Humboldt. To the south they are found along the Reese River, in Pine and Huntington Creek valleys, Independence Valley, and Diamond Valley. Along the Snake River Plain they inhabit the vicinity of American Falls Reservoir and, to the west, the stretch of the Snake River and its tributaries from Hammett, Idaho, to the vicinity of Vale, Oregon.

The physiographic history of the northern Great Basin explains many aspects of the current distribution of *Thomomys townsendii*. The Great Basin in the Miocene and Pliocene was characterized by moderate topographic relief and a trend toward warming climates. By the end of the Pliocene there were widespread grasslands and well-developed lacustrine and riparian environments (Axelrod 1950). As discussed previously, southern Oregon and Idaho had a history of lava flows. The Pleistocene topography of the Great Basin was in part characterized by lakes and rivers that formed a network of interconnected drainage basins as their water levels rose and fell with climatic fluctuations. Remnants of these Pliocene and Pleistocene hydrographic features are the deep and moist lacustrine and fluviatile soils of the type that *Thomomys townsendii* inhabits today. It was not until post-Wisconsin times that desert conditions prevailed in the Great Basin to the extent that some of these soils became uninhabitable.

The disjunct nature of the current distribution of *Thomomys townsendii* reflects the boundaries of these historical drainage basins and gaps in the distribution of the preferred soil type of the species (Rogers 1991: Fig. 1). A major division in the current distribution of *townsendii*, and one that is reflected in both genetic and morphological analyses of this and the companion study (Rogers 1991), lies between populations of the Snake River and Humboldt River drainages. These two regions of the *townsendii* distribution persist primarily on the remnants of historical Lake Idaho and Lake Lahontan drainage basins (Fig. 4). Today they are well isolated from each other by mountain ranges and scrub desert. Suitable habitat for *townsendii* was clearly once more abundant and continuous than it is today.

It is useful here to discuss historical events and hydrographic features relevant to establishing where suitable habitat once existed for *Thomomys townsendii*, including where the populations of the Snake River and Humboldt River may have once been connected. A historical network of drainage basins extended from Malheur Lake and the Owyhee River, south through Honey Lake Valley and Lake Lahontan, and east to the limits of the Bonneville basin. Remnants of Idaho Lake (late Pliocene/early Pleistocene) can also be included here as a potential continuation of lacustrine deposits extending from southwestern Oregon into southern Idaho (Fig. 4). Davis (1937) discusses the possibility of an eastern hydrographic link leading from the Humboldt River and Pleistocene Lake Lahontan into the Snake River drainage via the historical overflow at Red Rock Pass mentioned earlier. While this information will be useful in interpreting the general history of this species, both chronologically and geographically, the geological data for the area under consideration are sufficiently limited that the correlation of specific historical events with specific patterns found in *Thomomys townsendii* cannot be undertaken. A review of the distributions of other Great Basin organisms will be used to help reconstruct the historically suitable habitats and dispersal routes for *Thomomys townsendii.*

Evidence from fossil and Recent freshwater fish and invertebrate distributions not only substantiates the existence of hydrographically related connections through the Great Basin, but also suggests possible corridors through which *T. townsendii* could have colonized the northern part of its present range. In his study of the fish of the Lahontan basin, Snyder (1918) found that some fish species are most closely allied to the fauna of the southeastern Oregon lakes. He found potential affinities with the Bonneville basin also. Miller (1958) similarly discusses affinities between the Lahontan and Bonneville basins based on their respective fish faunas and notes that there may have been a historical connection between the basins in the Pliocene or early Pleistocene. Miller found the fauna of the upper Snake River to be sufficiently similar to the Bonneville basin to be included in the Bonneville system.

Taylor (1960) presented distributional information for fossil and Recent freshwater clams and snails that suggests a historical network of lakes and streams leading from the Snake River through southern Oregon and northeastern California into the western Great Basin. His evidence does not suggest a Lahontan-Bonneville link. The investigation by Bisson and Bond (1971) into the origin of the fish of Harney Basin in southeastern Oregon also supports the suggestion of a dispersal corridor from the Snake River to southeastern Oregon. An ancient connection between Harney Basin and Malheur River provided a route for fish dispersal and explains the faunal affinities seen today. Stream connections were obstructed, in part, by a late Pleistocene lava flow, damming the water of Harney Basin.

A detailed analysis of fish distributions and drainage basins of the intermountain region, including the Great Basin, is presented by Smith (1978). His data on the distributions of 83 fish species suggest a well-linked Klamath (southern Oregon)-Snake-Bonneville group and a separate group representing the Lahontan Basin. Analyses of the strengths of the barriers of 48 drainage basins suggest the following: (1) the Bonneville–upper Snake barrier is not a strong one, as evidenced by the Bonneville flood, (2) a Harney Basin–Snake River connection is suggested, (3) with the above two exceptions, colonization between the Snake River Basin and the Great Basin is rare, and (4) the Lahontan Basin shows low internal barrier strength, but the barrier between Lahontan and Bonneville is substantial.

While *T. townsendii* is not dependent on aquatic habitats, it exhibits a clear preference for lacustrine soils. The importance of the fish and mollusk evidence lies in describing a network of intermittently connected aquatic habitats in an area that has since been replaced by, or bisected by, lava flows and desert. These faunal studies and the brief geographic histories presented suggest potential links via Pleistocene hydrographic features on both the eastern and western ends of the current *townsendii* distribution. Details of the type of stream-to-stream network that must have existed to make gopher dispersal through southeastern Oregon possible are presented by Bisson and Bond (1971). Whether the route was as far east as Harney Basin or further west, through northeastern California, as suggested by Taylor's (1960) data, remains unclear. However, such a western hydrographic network appears to be a more viable corridor for pocket gopher dispersal than does the eastern Lahontan-Bonneville-Snake connection described for Great Basin fishes by Miller (1958). In fact, *Thomomys townsendii* is not known from the Lake Bonneville region, and, as outlined in the companion paper (Rogers 1991), there is no fossil evidence to suggest that this was ever part of the species range.

Morphological evidence presented by Davis (1937) suggests affinities between Pocatello (*T. t. similis*) and northeastern Nevada (*T. t. elkoensis*) animals and therefore an eastern link between northern and southern populations. To explain the apparent similarity, he proposed that the gophers followed the northern Bonneville shores into Idaho during the flood at Red Rock Pass (late Wisconsin). This study gives no clear indication of which route may have been taken. Only the color analysis shows any obvious similarity between populations of the two river systems, again between *T. t. elkoensis* and *T. t. similis* populations (Rogers 1991). However, it has been demonstrated that pelage data should be treated carefully in interpreting the historical patterns of pocket gophers. Studies of *T. bottae* (Patton et al. 1979, Smith and Patton 1980, Smith et al. 1983) have clearly shown the environmental influence on variation in pocket gopher coloration. In fact, the correspondence between pelage color and vegetation zone suggests that dark soils may be a factor these two subspecies have in common (Rogers 1991).

A further suggestion that Red Rock Pass did not serve as a dispersal corridor for *T. townsendii* is presented by Wells's (1983) discussion of montane conifer dispersal in the Great Basin. Red Rock Pass is one of the two topographically high connections between the high central plateau of the Great Basin and the western Rocky Mountains. The 1820-meter contour that Wells uses to outline these high mountain connections is graphically complementary to the distribution of *T. townsendii* and delineates historical and present-day boundaries to eastward dispersal.

DISCUSSION

Causes of genic homogeneity in fossorial rodents have been of particular interest to some authors. Nevo and Shaw (1972) and Nevo et al. (1974) have applied a model for selection for homozygosity in uniform subterranean environments to data for *Spalax ehrenbergi* and *Thomomys talpoides*, which both show very low levels of genic variation within and among populations. Other authors have found this selection model inappropriate for explaining the genetic patterns seen in *Thomomys*, arguing that features of pocket gopher population biology and stochastic factors explain their genetic divergence (Patton and Yang 1977, Patton 1981, Patton and Feder 1981). In contrast to the pattern of genic homogeneity seen in *talpoides*, variation within and among populations of *bottae* is high. Small, effective population size, nonrandom breeding, and migration rate in conjunction with historical changes in habitat, distribution, and population connectedness are cited as variables that have affected the genetic patterns of *T. bottae* and its relatives (Patton 1981). Results of this study are also consistent with the expected effects of these kinds of historical and population factors.

Patterns of Genetic Variation in *Thomomys townsendii*

The results of genic and karyotypic analyses of *Thomomys townsendii* reveal a pattern of extreme genetic homogeneity across a very broad and disjunct geographic range. The parameters of intrapopulation variation presented in this study categorize *townsendii* as being one of the least variable of the pocket gopher species studied. This species shows less variability (63% monomorphic) than other members of the *bottae*-group or *Thomomys* in general (*T. bottae:* 9% monomorphic, Patton and Yang 1977; *T. umbrinus:* 17%, Hafner et al. 1987; *T. talpoides:* 29%, Nevo et al. 1974).

Thomomys townsendii is also low in heterozygosity values and in average proportion of polymorphic loci relative to other rodents and to mammals in general (mean $H = .039$ for 50 mammals species examined, Avise and Aquadro 1982; also, see reviews by Selander et al. 1974, Powell 1975, Nevo 1978, Kilpatrick 1981). While the ranges in population values for P and H in *T. townsendii* overlap with those values in other gopher species, the means across populations in this species are among the lowest known in pocket gophers ($\bar{P} = .053$ and $\bar{H} = .012$). The means and ranges of values for closely related species are $\bar{P} = .334$ (.130-.565) and $\bar{H} = .093$ (.030-.169) for *Thomomys bottae* (Patton and Yang 1977) and $\bar{P} = .183$ (.043-.391) and $\bar{H} = .051$ (.008-.100) for *Thomomys umbrinus* (Hafner et al. 1987). Of the pocket gopher species exhibiting lower levels of within-population variability (Selander et al. 1974, Honeycutt and Williams 1982, Hafner and Barkley 1984), none maintains these low levels so uniformly over such a broad geographic range as does *Thomomys townsendii*.

Analyses of genic variation have also shown a high level of similarity ($\bar{S} = .956$) among the populations of *townsendii*. While these values are not unique among rodent studies (Avise 1974), they are extreme among *Thomomys* species (*T. bottae:* $\bar{S} = .81$, Patton and Yang 1977; *T. umbrinus:* $\bar{S} = .80$, Patton and Feder 1978, and Hafner et al. 1987; *T. talpoides:* $\bar{S} =$ .84, Nevo et al. 1974). Whereas values in *townsendii* are high in comparison to *bottae* as a whole, comparable levels of similarity are seen among the Great Basin populations of *bottae* (Patton and Yang 1977).

The nature of allozymic variation between populations in this species reflects the effects of rare variants at a small number of those loci examined. Wright's *F*-statistics show that populations are the units of greatest differentiation (highest F_{ST}) of any of the hierarchical levels compared. Within a geographic region, populations are more differentiated than are the subspecies of that region. However, all populations are united at a high level of genic similarity, $S = .939$. F_{ST} values for *Thomomys bottae* (Patton and Yang 1977) similarly show interpopulation differentiation representing a large component of the variation. This was true throughout the populations sampled in this study and within each of the geographic areas. Variation within this group of pocket gophers is generally greatest between the local units of any given area. The subspecific or regional categories within these species are thus internally quite heterogeneous.

The distinction between the two geographic regions is the only clear division at any level in *T. townsendii* and is due mostly to the effect of the single locus GOT-1, which is fixed for alternate alleles in populations of the Humboldt River/Honey Lake Valley versus the Snake River. The divergent populations within each of the regions are differentiated slightly from the remainder of their respective clusters by shifts in allele frequencies or by possession of an allele not found elsewhere. These few variants are of little absolute significance in distinguishing these populations from the remainder of their cluster, however. Patton and Feder (1981) showed in studies of *Thomomys bottae* at Hastings Reservation that genic differentiation between fields can be as high as the differentiation found between subspecies of a region in *T. townsendii* (*T. bottae* $F_{ST} = .142$, *T. townsendii* $F_{ST} = .151$ and .124). Considered in this context, the genic differentiation represented among the populations and subspecies within the two geographic units is remarkably low.

Results of the karyotypic analysis corroborate the findings of Wentworth and Sutton (1969) and Thaeler (1973) that the diploid number is 76 in all *Thomomys townsendii* subspecies. The only differentiation found within the otherwise totally biarmed karyotype is the presence of a single acrocentric pair of chromosomes in samples of *T. t. bachmani* and *T. t. relictus*. This pattern differs from the karyotypes reported by Wentworth and Sutton (1969) and Thaeler (1973), who group the chromosomes of all seven subspecies in the following way: 12 pairs of metacentrics, 22 pairs of submetacentrics, and 3 pairs of acrocentrics (FN = 142); the X chromosome is a large submetacentric, and the Y is a small acro- or subtelocentric. The lack of agreement with the published results can be explained, in part, by the lack of resolution in standard karyotypes. Without the aid of banded material, one is forced to use an arbitrary morphological classification. This may explain the disagreement in the numbers of chromosome pairs in each of the biarmed categories.

Although the distinction between uniarmed and biarmed chromosomes is more easily made, Wentworth and Sutton (1969) and Thaeler (1973) assigned three pairs of chromosomes to the uniarmed group, while one or none was so assigned in this study. The classification of the single uniarmed pair in *T. t. bachmani* and *T. t. relictus* remains somewhat ambiguous. However, the existence of such a variant in an otherwise karyotypically homogeneous species is almost to be expected. Variation seen in related species is often of this nature; arm number may be polymorphic or polytypic, while the diploid number remains constant within a given taxon (Patton 1972, Patton and Feder 1978, Patton and Sherwood 1982, Hafner et al. 1987). In addition, it is significant that the alternative karyotype is found in the Honey Lake Valley and in the neighboring *T. t. bachmani* populations which together form the western component of the Humboldt River region. Since southeastern Oregon samples of *T. t. bachmani* were not karyotyped in this study, it cannot be determined whether this pattern extends to those populations as well.

The discrepancy found in the morphology of the Y chromosome is less easily explained as preparation artifact. The Y chromosomes presented by Wentworth and Sutton (1969) are substantially larger than the dot chromosomes found in this study. As all other *bottae*-group karyotypes exhibit the minute acrocentric morphology in the Y chromosome (Patton and Dingman 1970, Patton 1972, Patton and Feder 1978, Hafner et al. 1987), it is probable that *Thomomys townsendii* also shows this pattern.

The amount of genic variation found in geomyids is often accompanied by greater karyotypic differentiation than that seen in *Thomomys townsendii* as well. Average similarity values within *Geomys bursarius* and *G. personatus* (data of Y. J. Kim presented by Nevo et al. 1974 and Selander et al. 1974) are .76 and .86, respectively, and both species are karyotypically polymorphic. Of the specimens analyzed allozymically by Kim (Selander et al. 1974), *G. bursarius* was represented by seven chromosomal forms (2n = 70, 72, 74 and FN = 68–74), and *G. personatus* was represented by five (2n = 68, 70 and FN = 68–74). Chromosomal variation in these species is due to Robertsonian changes (centric fusions and fissions), inversions, and translocations. Examination of contact zones in other studies of *G. bursarius* has shown that barriers to genetic exchange exist between some chromosomal forms (Honeycutt and Schmidly 1979, Tucker and Schmidly 1981, Bohlin and Zimmerman 1982). Within the *Thomomys talpoides* complex (Nevo et al. 1974), average genic similarity for the six karyotypic variants examined is .874. Thaeler believes that these morphs represent at least five separate species (Nevo et al. 1974). Within this complex diploid numbers range from 40 to 60, and chromosomal changes are typically due to Robertsonian changes and pericentric inversions.

Patton and Yang (1977) discussed differences in genetic variability of *T. bottae* and members of the *T. talpoides* complex. The pattern seen in *talpoides* is one of genic homogeneity and chromosomal differentiation to the point of reproductive isolation. Historical fragmentation and isolation of populations, bottlenecks, and founder effects may have resulted in the fixation of chromosomal rearrangements and fixation for alternate alleles where loci were once polymorphic. It is suggested that if reproductive isolation were attained, genic homogeneity would be maintained in these isolates. In contrast, chromosomal variability of *T. bottae* does not seem to affect reproductive isolation and interpopulation genic variability and within-population heterozygosities are high. Extensive range fragmentation is not suggested for *bottae*, gene flow is believed to have been less interrupted, and therefore genetic variability has been maintained. Historically, isolated populations of *bottae* were not chromosomally differentiated to the point of being reproductively isolated from other populations. Therefore, recontact with populations could have meant interbreeding, and bottlenecks that occurred due to isolation could have been overcome.

Evolutionary and Biogeographic History of *Thomomys townsendii*

While *Thomomys townsendii* does not share the genetic diversity characteristic of the *bottae*-group, its distributional history is more similar to that of *bottae*, undisturbed by glaciation, than to *talpoides*, whose boreal distribution was sculpted by glacial influences. Furthermore, the genic pattern in *townsendii* is remarkably similar to the kind of variation seen in the Great Basin populations of *bottae* (Patton and Yang 1977). The concordance between genic patterns of these two species in the same geographic area suggests that a similar history of biogeographic and stochastic events may have influenced their evolution in the Great Basin.

Given that historical biogeography may have affected the genetic patterns of *bottae* and *talpoides*, it is useful to understand the evolutionary history and affinities of *T. townsendii* before trying to interpret the patterns seen in this species. Studies by Bailey (1915), Thaeler (1980), and Patton and Smith (1981) support a dichotomy within *Thomomys*. Morphological, electromorphic, and karyological analyses place *Thomomys townsendii* in the *bottae*-group, which also contains *T. bottae*, *T. umbrinus*, and *T. bulbivorus*. This group, characterized as the "heavy-rostrum" group by Bailey (1915), can be distinguished karyotypically as having diploid numbers ranging from 74 to 88 (Thaeler 1980, Patton and Sherwood 1982). These characters distinguish the *bottae*-group from *T. talpoides* and other members of Bailey's (1915) "slender-rostrum" group (with diploid numbers ranging from 40 to 60 [Thaeler 1980]), including *T. clusius*, *T. idahoensis*, *T. mazama*, and *T. monticola*. Thaeler (1980) formalized this dichotomy by recognizing the slender- and heavy-rostrum groups as separate subgenera, *Thomomys* and *Megascapheus*, respectively. Patton and Smith (1981) did an electrophoretic analysis of six *Thomomys* species (*talpoides* and *monticola* in addition to the *bottae*-group species) and treated *T. townsendii* as part of the *bottae* unit; all alleles found in *townsendii* were also found in *bottae*. The same study determined that *bottae* and *townsendii* were a sister-group relative to *umbrinus*, that *townsendii* stemmed from within one of the major geographic units of *T. bottae*, and therefore that *bottae* was paraphyletic relative to *townsendii*. An analysis of cranial shape also supports this relationship (Patton and Smith 1989).

The evolutionary relationships of *bottae*, *townsendii*, and *umbrinus* are manifested in comparisons of karyotypic morphology and cellular DNA content, and in hybrid zone studies. The whole-arm heterochromatin found in *townsendii* resembles the pattern seen in *bottae* and is distinct from the interstitial heterochromatin characteristic of *umbrinus* (Patton and Sherwood 1982). Similarly, the amount of cellular DNA (*C*-value) found in *townsendii* is within the range found in *bottae* populations, whereas *umbrinus* has a higher *C*-value than would be expected for *T. bottae* with a similar karyotype (Sherwood and Patton 1982).

The karyotypic similarity between *bottae* and *townsendii* can be contrasted to the meiotically problematic structural rearrangements found between *bottae* and *umbrinus* (Patton 1973, Patton 1981), although studies of hybrid zones indicate that genetic introgression does not occur in either case. Both *townsendii* and *umbrinus* are known to hybridize minimally with *bottae* (12% and 11–15% hybrids, respectively). In *bottae*-*umbrinus* hybrids, F1 males are sterile, female fertility is reduced, and there is no genetic introgression (Patton 1973). While some F1 individuals from crosses of *bottae* and *townsendii* show normal reproductive characteristics, there is again no evidence for genic or morphological introgression into the parental populations (Patton et al. 1984). Both pairs of hybridizing species remain genetically isolated species, but only the *bottae*-*umbrinus* case is likely to be chromosomally mediated. The lack of genetic introgression in the presence of karyotypic similarity between *bottae* and *townsendii* suggests other influences. The significance of behavior in this case has been suggested (Patton et al. 1984).

The evolutionary affinities between *townsendii* and *bottae* are further reflected in information from studies of the distribution of gopher lice. Pocket gopher species often serve as hosts to more than one species of louse, and a single louse species may be found on more than one species of pocket gopher (Emerson and Price 1981). *T. townsendii* is known to be the host of one louse species, *Geomydoecus idahoensis*, except in two zones of hybridization with *bottae* (Patton et al. 1984). In Honey Lake Valley *T. townsendii relictus* hybridizes with *T. bottae saxatilis* and *T. bottae canus*. In these hybrid zones the *bottae* louse is found on some of the "pure" *townsendii* as well as on some of the hybrids. *G. idahoensis* belongs to the *oregonus* species group. Another member of this group, *Geomydoecus shastensis*, is morphologically very similar to *idahoensis* and, interestingly, is the louse found on *T. bottae saxatilis* (Price and Hellenthal 1980).

The level of chromosomal and genic similarity of *townsendii* and *bottae* and the evidence for paraphyly (Patton and Smith 1981, 1989) suggest that *Thomomys townsendii* was derived from *Thomomys bottae*. In addition, Bailey (1915) and Davis (1937) recognized the morphological affinities between the two species. Further examination of the nature of this morphological similarity demonstrates that there is basically no difference in cranial shape between the two species. It has been suggested that the difference in body size between the two species may have resulted in differences in demographic features that eventually created genetic isolation (Patton and Smith 1989).

What can be determined from the results of this study regarding the nature of the distribution of this species from the time of its founding population to the present? Was the range of *townsendii* once continuous over the northern Great Basin and subsequently fragmented by unsuitable habitats? Or is the distribution of *townsendii* the result of relatively recent dispersal from one segment of the species range?

The concordance of genetic data with historical and biogeographic patterns has been emphasized in other pocket gopher studies. Patton (1981) discusses the influences of history and features of pocket gopher population biology in the context of the agreement of karyotypic and genic data for *Thomomys* *bottae.* Morphological patterns of differentiation, however, are often best explained by environmental factors such as quality and color of the soil and nutritional value of available food and probably do not provide much information regarding the evolutionary history of *T. bottae* (Smith and Patton 1980). Further studies (Patton and Brylski 1987, Smith and Patton 1988) have demonstrated that while pelage coloration and body size are strongly influenced by environmental factors, cranial shape variation is more likely to represent genetically based changes. In the absence of an analysis focusing on cranial shape in *Thomomys townsendii*, the results of the genetic analyses will be emphasized in developing a historical scenario for this species.

While the nature of the historical distribution of *Thomomys townsendii* is not easily determined by the results of this study and its companion paper (Rogers 1991), evidence does exist that eliminates some possibilities and suggests others. A description of the historical biogeography of the northern Great Basin that focuses on the changes in and the availability of suitable habitat for *Thomomys townsendii* has been presented. It indicates that the wetter climates of the Pleistocene of the northern Great Basin produced a network of lacustrine and fluviatile soils that were occasionally continuous until desert conditions prevailed, rendering some of these soils uninhabitable. The continuity of these habitats could have provided historical corridors for dispersal.

However, while these historical connections can be reconstructed, it is unlikely that the species could have maintained a continuous range over most of the northern Great Basin at one time. Rather, it seems feasible that after the origin from *T. bottae*, segments of the range of *T. townsendii* were connected to various degrees at different points in its distributional history. Barriers to the continuity of the range probably arose at different times in different places. As climates increased in aridity and lakes receded, some areas became unable to support gopher populations, and *townsendii* remained along rivers and receding lake shores. Further fragmentation and isolation of some sections of the range of *T. townsendii* probably occurred with the intrusion of lava flows. Information from this study supports the idea that a fragmented distribution has always been characteristic of this species and also suggests in which areas a more continuous distribution may have existed historically.

For instance, analyses of the genetic data indicate that populations of the Snake River belong to a very cohesive cluster ($\bar{S} = .984$) despite the geographical separation of the *T. t. similis* populations by more than 100 miles. Fossil evidence from Wilson Butte Cave (Gruhn 1961, Rogers 1991) suggests that continuity between the western (*T. t. owyhensis* and *T. t. townsendii*) and eastern (*T. t. similis*) parts of the Snake River distribution may have existed fairly recently. Only the eastern *T. t. townsendii* population (22) is clearly differentiated from the other Snake River populations. Most of the samples from this region differ from each other in allele frequencies and, in one case, in the presence of a rare ADA allele in low frequency. The magnitude of the differentiation of the Grandview *T. t. townsendii* population (22) is primarily due to the appearance of the PGM *c* allele in relatively high frequency (.625). This allele was not encountered in other populations. The reason for the divergence of this population is not clear, but geologic evidence suggests that historically this area may have been isolated by lava flows (Malde and Powers 1962, Malde 1965).

While variation in the Humboldt River region is very limited, more genetic differentiation is seen among these populations than among those of the Snake River region. The only karyotypic differentiation documented in this study is seen in representatives of two of the Humboldt River subspecies. Analyses of the populations of this region resulted in a cluster of six genetically very similar ($S > .97$) populations and three more differentiated populations: Lovelock, Narrows, and Austin. The members of the more cohesive cluster include *T. t. elkoensis*, two of the four *T. t. bachmani* populations, and the Honey Lake Valley (*T. t. relictus*) populations. These samples are differentiated from one another by the presence of one to four alleles in low frequency that are not found in other populations of that cluster.

Despite their peripheral location, Honey Lake Valley populations display affinities to the Humboldt River populations as they did in the morphological analyses of the companion paper (Rogers 1991). Examination of the *F*-statistics further supports the inclusion of Honey Lake Valley populations in the Humboldt River geographic region. Subunits within regions show less differentiation when Honey Lake Valley is regarded as a part of the Humboldt River region. Greater genic similarity is found between Honey Lake Valley populations and certain Humboldt River populations than among some Humboldt River populations. The same is true at the subspecific level. Historically, Honey Lake Valley was part of Lake Lahontan, so the affinity to these populations is not surprising. Only the karyotypic analysis shows Honey Lake Valley populations deviating from most other populations in that *T. t. relictus* and *T. t. bachmani* possess a single acrocentric pair among an otherwise biarmed complement of chromosomes.

The genic divergence of two of the *T. t. bachmani* populations (Lovelock and Narrows) is due to the prevalence of a single allele not found elsewhere. The *T. t. nevadensis* sample from Austin is the most differentiated population of the Humboldt River region. The magnitude of this divergence is attributable almost entirely to a fixed difference for a PREALB allele. This allele is otherwise only present, in moderately low frequency (.200), in a single *T. t. elkoensis* population. Austin and Narrows animals are consistently differentiated from the other populations in both genetic and morphological analyses (Rogers 1991). This may reflect their peripheral position relative to the Lahontan drainage system. Although located in a Pleistocene lake basin, Narrows is actually outside the Lahontan hydrographic basin, but it was probably once connected to the main basin. The divergence of this population from other units of this region probably reflects its isolation due to a combination of encroaching desert regions and the influence of the drainage divide.

Austin is located in the Reese River valley, south of the Humboldt River. The Reese River was a tributary of the Humboldt River during Lahontan times but was not represented by a pluvial lake (Morrison 1965), suggesting relative aridity in this basin even during pluvial times. Today the Reese River reaches the Humboldt only intermittently so that habitable areas for *T. townsendii* may be restricted to the southern portions of this valley. Isolation by inadequate habitat may have contributed to separation and divergence of this population. Furthermore, *T. talpoides* is currently found in this valley only 24 miles north of Austin. The presence of this species may have subsequently enforced existing physical barriers.

Another possible explanation for the differentiation exists if this area was one of the earliest colonized subsequent to the derivation of *townsendii* from *bottae*. Davis (1937) remarked that, of the *townsendii* subspecies, *T. t. nevadensis* is structurally most similar to *bottae*. If the Reese River valley were colonized from the south rather than from the Humboldt River to the north, it is possible that distribution through this area was never continuous with the remainder of the Humboldt River distribution, or that this area was isolated relatively early.

Much of the information presented above regarding genic differentiation among *T. townsendii* populations has a morphological counterpart from the analyses of cranial and pelage differentiation (Rogers 1991). However, relative to the genic data, morphological characters reflect a general pattern of more overlap with fewer strongly differentiated populations. As one would expect, some aspects of the biogeographic history of *T. townsendii* populations seem to be more closely reflected in the genic data. For instance, the four most divergent populations (Austin, Narrows, Grandview-*t.*, and Lovelock) all have an alternative allele as the predominant one at some locus. This kind of pattern is sometimes associated with isolation, whether it be a result of a founder event or range fragmentation. For some of these populations the features maintaining biogeographic isolation are obvious, although the mechanism by which isolation began is difficult to determine. The factors that might have contributed to the isolation of the Austin, Narrows, and Grandview-*t.* populations have already been discussed. Explaining the extent of differentiation seen in the *T. t. bachmani* population at Lovelock is more problematic. Since this area is part of the large and continuous Pleistocene Lake Lahontan, reasons for isolation and differentiation are not clear. However, it is peripherally located in the species range, and the nearest neighboring specimens examined in this study are from about 75 miles up the Humboldt River.

Thomomys townsendii is characterized not only by genetic homogeneity within populations, but by shifts in allele frequencies and appearance of rare alleles in high frequencies among populations. In addition, patterns of genic similarity between populations do not correspond to geographic distance, and populations of different subspecies or geographic subunits are often more similar than are other members of the same subspecies. These features do not suggest a broadly continuous species distribution historically. It is not surprising that this pattern instead suggests the effects of drift and independent evolution on population isolates that arose from the colonization of new areas or by the fragmentation of once more continuous habitat. Pocket gophers are strongly susceptible to drift due to small, effective population size and their inability to cross various environmental barriers, which may include other gopher species.

A reasonable explanation of the events in the origin and distribution of *Thomomys townsendii* begins with a relatively recent derivation from *Thomomys bottae*. In their analysis of *T. bottae* genic evolution, Patton and Smith (1981) discuss what appears to be a decreased rate of allozymic change in *T. townsendii*. However, they suggest that their results probably do not represent actual rate changes, but reflect low levels of within-population variation in *T. townsendii*. They hypothesize that this homogeneity is the result of a founder event and subsequent isolation, and later morphological studies suggest that the derivation from *bottae* was a relatively recent event (Patton and Smith 1989). While sufficient information is not available to pinpoint when and where *townsendii* arose from *bottae*, an origin from the southern part of the current *townsendii* distribution has been suggested. Davis (1937) noted the similarity between *bottae* and the most southern subspecies, *T. t. nevadensis*, and later stated that *townsendii* had probably moved into Idaho from the south (Davis 1939). In addition, in comparing *T. townsendii* to *T. bottae* populations, Patton and Smith (1989) show that *townsendii* is genetically most similar to *bottae* populations from central and southern California.

The low level of variation seen throughout *T. townsendii* suggests that stages of isolation and subsequent genetic drift followed the divergence from *T. bottae*. Derivation from a single highly homozygous founding population would provide the genetic background necessary for dominant alleles to be maintained across the distribution despite discontinuities that inevitably arose after *T. townsendii* colonized the area. High interpopulation similarity suggests that low levels of genic variability were maintained as the founding population eventually dispersed through the Great Basin. The remnants of Pleistocene lakes served as a corridor for the dispersal of the species through northern Nevada, northeastern California, and southeastern Oregon and possibly into lake beds to the west of the present Oregon distribution, judging from fossil evidence (Allison 1966). Colonization of this area probably proceeded as a series of founder events with portions of the distribution becoming fragmented. The background of genetic homogeneity was maintained with diversification in the form of allelic variants. The fixed difference at the GOT-1 locus and the homogeneity seen among the Snake River populations suggest that this region was probably colonized by a single founding population from the Humboldt River region. Subsequent to dispersal of the species across the Snake River plain, discontinuities to the range arose and populations became slightly differentiated.

The relative homogeneity of the Snake River populations also suggests this region has had less time to differentiate than has the Humboldt River region. To demonstrate the relative difference in age among and between the Snake River and Humboldt River areas, estimated divergence times between populations were calculated and averaged for these two major geographic regions. Values generated for Nei's genetic distance and the methods of Nei (1971) as described by Patton and Yang (1977) were used for these estimates. An average divergence time between populations of these two geographic units is 255,400 years before present (maximum, 475,000 YBP; minimum, 190,000 YBP). The same value, calculated for populations of the Humboldt River region, is 92,083 years (maximum, 300,000 YBP; minimum, 5,000 YBP), while that for the Snake River populations is 27,143 years (maximum, 95,000 YBP; minimum, 0 YBP). As additional reference points, these divergence times were adjusted using the albumin immunological distance method (Sarich and Cronin 1976, Sarich 1977), again following Patton and Yang (1977). These estimates show average divergence time between populations of the two river systems to be 1,072,680 YBP; among Humboldt River populations the average divergence time is 386,749 YBP, and within the Snake River system it is 114,001 YBP. While these values present very different approximations of divergence times within *Thomomys townsendii*, they do indicate a general time frame and what the sequence of events might have been. These estimates suggest that divergence among the Snake River populations occurred subsequent to the isolation between the northern and southern parts of the distribution and after diversification of the Humboldt River populations had begun.

Physical aspects of the two regions may have also contributed to the different degrees of morphological and genetic differentiation seen between the Humboldt River and Snake River regions. The greater biogeographic diversity and increased aridity of the Humboldt River region may have promoted isolation and differentiation in this area. Features of the habitat, particularly soil color and quality, may be more homogeneous along the Snake River drainage and influential in maintaining morphological homogeneity.

Systematic Conclusions

The genic data are the strongest indicators of differentiation that is greatest between the regions represented biogeographically by the Humboldt River and the Snake River drainage systems. One fixed difference (GOT-1) and the appearance of additional alleles at other loci separate these groups genically. Distinction between these two regions exists but is less apparent in discriminant function analyses of cranial characters (Rogers 1991). This pattern of differentiation does not correspond to the currently recognized seven subspecific units, originally described by Davis (1937). The data presented here and in the companion study (Rogers 1991) show that, in some cases, greater morphological and genetic differentiation has been found among samples within a subspecies than between subspecies. This is most apparent in the Humboldt River group, whereas the Snake River region represents a more homogeneous unit. The variants observed in this study are usually quite subtle and do not warrant taxonomic distinction.

The population from Austin deserves special consideration here. These individuals are clearly differentiated morphologically (Rogers 1991) and genically. The historical biogeography of the *T. t. nevadensis* distribution and the presence of *T. talpoides* to the north suggest effective and possibly early barriers to gene flow with *Thomomys townsendii* populations to the north. The intermediate level of differentiation seen in the Austin sample is noteworthy in the context of understanding evolution within this species but does not warrant the level of distinction given to the two major geographic regions.

The absence of genetic variation in *Thomomys townsendii* is most remarkable considering the phylogenetic affinities between *townsendii* and *T. bottae*. The patterns of genetic variability found in *T. townsendii* and *T. bottae* are strikingly dissimilar. *Thomomys bottae* is characterized by extreme interpopulation differentiation in allozymes (Patton and Yang 1977), with an average Rogers' *S* between populations of .81. Similarly, karyotypic variability is great, consisting primarily of variation in arm number. These variants are the result of additions and/or deletions of heterochromatic arms (Patton and Sherwood 1982). Allozymic patterns of differentiation are concordant with geographic patterns of change in karyotype (Patton and Yang 1977, Patton and Smith 1981). Karyotypic and allozymic patterns are also concordant in *T. townsendii* in that they show homogeneity across geography. The type of chromosomal polymorphism found in *T. townsendii* is characteristic of species in the *bottae*-group and apparently does not act as a fertility barrier (Patton and Sherwood 1982). It is therefore unlikely that such variants are of much consequence in the evolutionary differentiation within *townsendii*.

In summary, *Thomomys townsendii* can be characterized as having undergone little intraspecific morphological and genetic differentiation since its origin from an ancestral stock, probably *Thomomys bottae*. Based on cranial, external, and pelage measurements, the species is quite homogeneous (Rogers 1991). The only chromosomal differences in *T. townsendii* involve a single uniarmed pair in an otherwise completely biarmed complement. The variation found in the genic data is primarily based on shifts in allele frequencies in some populations and the presence of rare alleles in others. *F*-statistics indicate that genic differentiation is greatest between populations and slightest between the subspecies within each geographic region. Subspecific integrity is not maintained by any units within the two regions. Given this high level of homogeneity, a conservative interpretation of the details of differentiation is necessary in assessing meaningful taxonomic categories within *Thomomys townsendii.*

The only pattern that is concordant among the data sets presented here and in the accompanying paper (Rogers 1991) is the break between the Snake River populations and those of Honey Lake Valley and the Humboldt River. Discriminant function analyses based on cranial characters show some differentiation between these two groups, although overlap exists (Rogers 1991). A fixed difference at the GOT-1 locus provides a clear split between these two regions despite their generally high genic similarity ($S = .94$).

The evidence from this study suggests that only two geographical units can appropriately be given subspecific distinction. The ranges of these units correspond to (1) the Snake River Plain of Idaho and southeastern Oregon and (2) the Humboldt and Quinn River drainage systems in Nevada, southeastern Oregon (vicinity of Malheur Lake and Lake Alvord), and Honey Lake Valley, California. Within each of these regions there is local differentiation in some characters, but particular populations or subregions are not consistently delineated across many characters and modes of analysis (Rogers 1991). The currently recognized subspecies *T. t. bachmani, T. t. elkoensis, T. t. nevadensis,* and *T. t. relictus* are herein regarded as synonyms of *Thomomys townsendii nevadensis* Merriam, 1897, which has priority. The Snake River populations, representing *T. t. owyhensis, T. t. similis,* and *T. t. townsendii,* are treated as synonyms of *Thomomys townsendii townsendii* (Bachman 1839).

Thomomys townsendii nevadensis Merriam

Thomomys nevadensis Merriam, 1897, Proceedings of the Biological Society of Washington 11: 213. Type from Austin, Nevada; United States National Museum, Biological Survey Collection no. $\frac{25001}{32413}$.

Thomomys townsendi nevadensis Bailey, 1915, North American Fauna 39:44.

Thomomys relictus Grinnell, 1926, University of California Publications in Zoology 30(1):2. Type from valley of Susan River two miles south of Susanville, Lassen County, California; Museum of Vertebrate Zoology no. 35271.

Thomomys townsendii relictus Grinnell, 1933, University of California Publications in Zoology 40(2): 137.

Thomomys townsendii bachmani Davis, 1937, Journal of Mammalogy 18(2): 150. Type from Quinn River Crossing, 4100 feet altitude, Humboldt County, Nevada; Museum of Vertebrate Zoology no. 7855.

Thomomys townsendii elkoensis Davis, 1937, Journal of Mammalogy 18(2): 151. Type from Evans, Eureka County, Nevada; Museum of Vertebrate Zoology no. 70583.

Thomomys umbrinus bachmani Hall, 1981, The Mammals of North America 1: 477.

Thomomys umbrinus elkoensis Hall, 1981, The Mammals of North America 1: 482.

Thomomys umbrinus nevadensis Hall, 1981, The Mammals of North America 1: 488.

Thomomys umbrinus relictus Hall, 1981, The Mammals of North America 1:492.

Thomomys townsendii townsendii (Bachman)

Geomys townsendii Bachman, 1839, (from Richardson's manuscripts) Journal of the Academy of Natural Sciences, Philadelphia 8(1):105. Type locality "Columbia River" is incorrect according to Bailey (1915:42), who feels the locality is near Nampa, Idaho; Academy of Natural Sciences Philadelphia no. 147.

Thomomys townsendii Allen, 1893, Bulletin of the American Museum of Natural History 5(5): 61.

Thomomys nevadensis atrogriseus Bailey, 1914, Proceedings of the Biological Society of Washington 27: 118. Type from Nampa, Idaho; United States National Museum, Biological Survey Collection no. 181, 196.

Thomomys townsendi townsendi Bailey, 1915, North American Fauna 39: 42.

Thomomys townsendii townsendii Whitlow and Hall, 1933, University of California Publications in Zoology 40(3): 255.

Thomomys townsendii owyhensis Davis, 1937, Journal of Mammalogy 18(2): 154. Type from Castle Creek, eight miles south of Oreana, Owyhee County, Idaho; Museum of Vertebrate Zoology no. 67490.

Thomomys townsendii similis Davis, 1937, Journal of Mammalogy 18(2): 155. Type from Pocatello, Bannock County, Idaho; Museum of Vertebrate Zoology no. 46507.

Thomomys umbrinus owyhensis Hall, 1981, The Mammals of North America 1: 489.

Thomomys umbrinus similis Hall, 1981, The Mammals of North America 1: 494.

Thomomys umbrinus townsendii Hall, 1981, The Mammals of North America 1: 495.

ACKNOWLEDGMENTS

I give special thanks to J. L. Patton for his support, guidance, and encouragement through all phases of this project and for the important contributions he made to the various drafts of this paper. D. B. Wake, W. Clemens, W. E. Bemis, B. D. Patterson, and W. T. Stanley read this and earlier drafts of the manuscript and provided useful criticism. R. D. Sage, M. F. Smith, M. Frelow, and E. Tang provided advice and assistance during the electrophoretic analyses. I thank D. S. Rogers for his guidance through my chromosome work and for his valuable support. N. Jo, M. A. Barros, and S. W. Sherwood also gave helpful suggestions on chromosome preparations. Many ranchers and landowners of the northern Great Basin were helpful and cooperative in my collecting efforts. For their support and confidence I thank my parents, Owen and Hally Rogers. I extend deep appreciation to W. E. Bemis for providing invaluable assistance in the field and consistent support throughout this project. This study and its companion paper are based on a thesis completed in partial fulfillment of requirements for the M.A. degree in the Department of Zoology, University of California, Berkeley. Financial support for this research was provided by the Department of Zoology, Museum of Vertebrate Zoology (two Louise M. Kellogg Grants-in-Aid), and National Science Foundation grant DEB 81-09677 to J. L. Patton. The Department of Anatomy, University of Chicago, and Field Museum of Natural History generously provided use of their facilities.

LITERATURE CITED

ALLEN, J. A. 1893. Descriptions of four new species of *Thomomys*, with remarks on other species of the genus. Bulletin of the American Museum of Natural History 5(5): 47–68.

ALLISON, I. S. 1966. Fossil Lake, Oregon. Its geology and fossil faunas. Oregon State Monographs, Studies in Geology 9: 1–48.

ANTEVS, E. 1948. Climatic changes and pre-white man. Bulletin of the University of Utah 38(20), Biological Series 10(7): 168–191.

AVISE, J. C. 1974. Systematic value of electrophoretic data. Systematic Zoology 23: 465–481.

AVISE, J. C., AND C. F. AQUADRO. 1982. A comparative summary of genetic distances in the vertebrates. Patterns and correlations. Evolutionary Biology 15: 151–185.

AXELROD, D. I. 1950. Studies in late Tertiary paleobotany. Contributions to Paleontology, Carnegie Institute of Washington, Publication 590: 1–323.

BACHMAN, J. 1839. Additional remarks on the genus *Lepus;* with corrections of a former paper, and descriptions of other species of quadrupeds found in North America. Journal of the Academy of Natural Sciences, Philadelphia 8: 75–105.

BAILEY, V. 1914. Eleven new species and subspecies of pocket gophers of the genus *Thomomys*. Proceedings of the Biological Society of Washington 27: 115–118.

———. 1915. Revision of the pocket gophers of the genus *Thomomys*. North American Fauna No. 39: 1–136.

BENDER, M. A., AND E. H. Y. CHU. 1963. The chromosomes of Primates. Pages 261–310 *in* J. Buettner-Janusch, ed., Evolutionary and genetic biology of Primates. Vol. I. Academic Press, New York.

BENSON, L. V. 1978. Fluctuations in the level of pluvial Lake Lahontan during the last 40,000 years. Quaternary Research 9: 300–318.

BISSON, P. A., AND C. E. BOND. 1971. Origin and distribution of the fishes of Harney Basin, Oregon. Copeia 2: 268–281.

BOHLIN, R. G., AND E. G. ZIMMERMAN. 1982. Genic differentiation of two chromosome races of the *Geomys bursarius* complex. Journal of Mammalogy 63: 218–228.

BROECKER, W. S., AND A. KAUFMAN. 1965. Radiocarbon chronology of Lake Lahontan and Lake Bonneville II, Great Basin. Geological Society of America Bulletin 76: 537–566.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora—vascular plants of the Intermountain West, USA. Vol. 1. Hafner Publishing Co., New York. 270 pp.

DAVIS, W. B. 1937. Variations in Townsend pocket gophers. Journal of Mammalogy 18: 145–158.

———. 1939. The Recent mammals of Idaho. Caxton Printers, Caldwell, Idaho. 400 pp.

———. 1940. Distribution and variation of pocket gophers (genus *Geomys*) in the southwestern United States. Texas A & M College, Texas Agricultural Experiment Station Bulletin 590: 1–38.

EMERSON, K. C., AND R. D. PRICE. 1981. A host-parasite list of the Mallophaga on mammals. Miscellaneous Publications of the Entomological Society of America 12: 1–72.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. American Naturalist 106: 645–668.

FITCH, W. M., AND E. MARGOLIASH. 1967. Construction of phylogenetic trees. Science 155: 279–284.

GILBERT, G. K. 1890. Lake Bonneville. Monographs of the U.S. Geological Survey 1: 1–438.

GRINNELL, J. 1926. The pocket gopher of Honey Lake Valley. University of California Publications in Zoology 30: 1–6.

———. 1927. Geography and evolution in the pocket gophers of California. Annual Report of the Smithsonian Institution, 1926, Publication 2894: 343–355.

———. 1933. Review of the Recent mammal fauna of California. University of California Publications in Zoology 40: 71–234.

GRUHN, R. 1961. The archaeology of Wilson Butte Cave south-central Idaho. Occasional Papers of the Idaho State College Museum 6: 1–202.

HAFNER, M. S., AND L. J. BARKLEY. 1984. Genetics and natural history of a relictual pocket gopher, *Zygogeomys* (Rodentia: Geomyidae). Journal of Mammalogy 65: 474–479.

Hafner, M. S., J. C. Hafner, J. L. Patton, and M. F. Smith. 1987. Macrogeographic patterns of genetic differentiation in the pocket gopher *Thomomys umbrinus*. Systematic Zoology 36: 18–34.

Hall, E. R., 1946. Mammals of Nevada. University of California Press, Berkeley. xi + 710 pp.

_____. 1981. The mammals of North America. Vol. 1. John Wiley and Sons, New York. xv + 600 + 90 pp.

Honeycutt, R. L., and D. J. Schmidly. 1979. Chromosomal and morphological variation in the plains pocket gopher, *Geomys bursarius*, in Texas and adjacent states. Occasional Papers, The Museum, Texas Tech University 58: 1–54.

Honeycutt, R. L., and S. L. Williams. 1982. Genic differentiation in pocket gophers of the genus *Pappogeomys* with comments on intergeneric relationships in the subfamily Geomyinae. Journal of Mammalogy 63: 208–217.

Ingles, L. G. 1950. Pigmental variations in populations of pocket gophers. Evolution 4: 353–357.

Kilpatrick, C. W. 1981. Genetic structure of insular populations. Pages 28–59 *in* M. H. Smith and J. Joule, eds., Mammalian population genetics. University of Georgia Press, Athens.

Kuntz, M. A., E. C. Spiker, M. Ruben, D. E. Champion, and R. H. Lefebvre. 1986. Radiocarbon studies of latest Pleistocene and Holocene lava flows of the Snake River Plain, Idaho: data, lessons, interpretations. Quaternary Research 25: 163–176.

Lee, M. R., and F. F. B. Elder. 1980. Yeast stimulation of bone marrow mitosis for cytogenetic investigations. Cytogenetics and Cell Genetics 26: 36–40.

Malde, H. E. 1965. Snake River Plain. Pages 255–263 *in* H. E. Wright, Jr., and D. G. Frey, eds., The Quaternary of the United States. Princeton University Press, Princeton, New Jersey.

_____. 1968. The catastrophic late Pleistocene Bonneville flood in the Snake River Plain, Idaho. United States Geological Survey Professional Paper 596: 1–52.

Malde, H. E., and H. A. Powers. 1962. Upper Cenozoic stratigraphy of western Snake River Plain, Idaho. Geological Society of America Bulletin 73: 1197–1220.

Meinzer, O. E. 1922. Map of the Pleistocene lakes of the Basin and Range Province and its significance. Bulletin of the Geological Society of America 33: 541–552.

Merriam, C. H. 1895. Monographic revision of the pocket gophers family Geomyidae (exclusive of the species of *Thomomys*). North American Fauna 8: 1–258.

_____. 1897. Descriptions of eight new pocket gophers of the genus *Thomomys*, from Oregon, California, and Nevada. Proceedings of the Biological Society of Washington 11: 213–216.

Mifflin, M. D., and M. M. Wheat. 1979. Pluvial lakes and estimated pluvial climates of Nevada. Nevada Bureau of Mines and Geology Bulletin 94: 1–57.

Miller, R. R. 1958. Origin and affinities of the freshwater fish fauna of western North America. Pages 187–222 *in* C. L. Hubbs, ed., Zoogeography. American Association for the Advancement of Science Publication 51. Horn-Shafer Co., Baltimore, Maryland.

Morrison, R. B. 1965. Quaternary geology of the Great Basin. Pages 265–285 *in* H. E. Wright, Jr., and D. G. Frey, eds., The Quaternary of the United States. Princeton University Press, Princeton, New Jersey.

Nei, M. 1971. Interspecific gene differences and evolutionary time estimated from electrophoretic data on protein identity. American Naturalist 105: 385–398.

_____. 1973. Analysis of gene diversity in subdivided populations. Proceedings of the National Academy of Sciences 70(12): 3321–3323.

_____. 1977. F-statistics and analysis of gene diversity in subdivided populations. Annals of Human Genetics 41: 225-233.

Nevo, E. 1978. Genetic variation in natural populations: patterns and theory. Theoretical Population Biology 13: 121–177.

Nevo, E., and C. R. Shaw. 1972. Genetic variation in a subterranean mammal, *Spalax ehrenbergi*. Biochemical Genetics 7: 235–241.

Nevo, E., Y. J. Kim, C. R. Shaw, and C. S. Thaeler, Jr. 1974. Genetic variation, selection and speciation in *Thomomys talpoides* pocket gophers. Evolution 28: 1–23.

Patton, J. L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). Journal of Mammalogy 48: 27–37.

_____. 1970. Karyotypic variation following an elevational gradient in the pocket gopher, *Thomomys bottae grahamensis* Goldman. Chromosoma (Berlin) 31: 41–50.

_____. 1972. Patterns of geographic variation in karyotype in the pocket gopher, *Thomomys bottae* (Eydoux and Gervais). Evolution 26: 574–586.

_____. 1973. An analysis of natural hybridization between the pocket gophers, *Thomomys bottae* and *Thomomys umbrinus*, in Arizona. Journal of Mammalogy 54: 561–584.

_____. 1981. Chromosomal and genic divergence, population structure, and speciation potential in *Thomomys bottae* pocket gophers. Pages 255–295 *in* O. A. Reig, ed., Ecologia y Genetica de la Especiacion Animal. Equinoccio, Caracas, Venezuela.

Patton, J. L., and P. V. Brylski. 1987. Pocket gophers in alfalfa fields: causes and consequences of habitat-related body size variation. American Naturalist 130: 493–506.

Patton, J. L., and R. E. Dingman. 1970. Chromosome studies of pocket gophers, genus *Thomomys*. II. Variation in *T. bottae* in the American southwest. Cytogenetics 9: 139–151.

Patton, J. L., and J. H. Feder. 1978. Genetic divergence between populations of the pocket gopher, *Thomomys umbrinus* (Richardson). Zeitschrift für Saugetierkunde 43: 17–30.

_____. 1981. Microspatial genetic heterogeneity in pocket gophers: non-random breeding and drift. Evolution 35: 912–920.

Patton, J. L., and S. W. Sherwood. 1982. Genome evolution in pocket gophers (Genus *Thomomys*) I. Heterochromatin variation and speciation potential. Chromosoma (Berlin) 85: 149–162.

Patton, J. L., and M. F. Smith. 1981. Molecular evolution in *Thomomys*: phyletic systematics, paraphyly, and rates of evolution. Journal of Mammalogy 62: 493–500.

______. 1989. Population structure and the genetic and morphologic divergence among pocket gopher species (genus *Thomomys*). Pages 284–304 *in* D. Otte and J. Endler, eds., Speciation and its consequences. Sinauer Associates, Inc., Sunderland, Massachusetts.

PATTON, J. L., AND S. Y. YANG. 1977. Genetic variation in *Thomomys bottae* pocket gophers: macrogeographic patterns. Evolution 31: 697–720.

PATTON, J. L., J. C. HAFNER, M. S. HAFNER, AND M. F. SMITH. 1979. Hybrid zones in *Thomomys bottae* pocket gophers: genetic, phenetic, and ecologic concordance patterns. Evolution 33: 860–876.

PATTON, J. L., M. F. SMITH, R. D. PRICE, AND R. A. HELLENTHAL. 1984. Genetics of hybridization between the pocket gophers *Thomomys bottae* and *Thomomys townsendii* in northeastern California. Great Basin Naturalist 44: 431–440.

PRAGER, E. M., AND A. C. WILSON. 1976. Congruency of phylogenies derived from different proteins. A molecular analysis of the phylogenetic position of cracid birds. Journal of Molecular Evolution 9: 45–57.

PENNEY, D. E., AND E. G. ZIMMERMAN. 1976. Genic divergence and local population differentiation by random drift in the pocket gopher genus *Geomys*. Evolution 30: 473–483.

POWELL, J. R. 1975. Protein variation in natural populations of animals. Pages 79–119 *in* T. Dobzhansky, M. K. Hecht, and W. C. Steere, eds., Evolutionary biology. Vol. 8. Plenum Press, New York.

PRICE, R. D., AND R. A. HELLENTHAL. 1980. The *Geomydoecus oregonus* complex (Mallophaga: Trichodectidae) of the western United States pocket gophers (Rodentia: Geomyidae). Proceedings of the Entomological Society of Washington 82: 25–38.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics VII. University of Texas Publication 7213: 145–153.

ROGERS, M. A. 1991. Evolutionary differentiation within the northern Great Basin pocket gopher, *Thomomys townsendii*. I. Morphological variation. Great Basin Naturalist 51: 109–126.

RUSSELL, I. C. 1885. Geological history of Lake Lahontan, a Quaternary lake of northwestern Nevada. Monographs of the United States Geological Survey 11: 1–288.

SARICH, V. M. 1977. Rates, sample sizes, and the neutrality hypothesis for electrophoresis in evolutionary studies. Nature 265: 24–28.

SARICH, V. M., AND J. E. CRONIN. 1976. Molecular systematics of the Primates. Pages 141–170 *in* M. Goodman, R. E. Tashian, and J. H. Tashian, eds., Molecular anthropology. Plenum Press, New York.

SELANDER, R. K., D. W. KAUFMAN, R. J. BAKER, AND S. L. WILLIAMS. 1974. Genic and chromosomal differentiation in pocket gophers of the *Geomys bursarius* group. Evolution 28: 557–564.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics VI. University of Texas Publication 7103: 49–90.

SHERWOOD, S. W., AND J. L. PATTON. 1982. Genome evolution in pocket gophers (genus *Thomomys*). II. Variation in cellular DNA content. Chromosoma (Berlin) 85: 163–179.

SMITH, G. R. 1978. Biogeography of intermountain fishes. Pages 17–42 *in* K. T. Harper and J. L. Reveal, eds., Intermountain biogeography: a symposium. Great Basin Naturalist Memoirs 2: 1–268.

SMITH, M. F., AND J. L. PATTON. 1980. Relationships of pocket gopher (*Thomomys bottae*) populations of the lower Colorado River. Journal of Mammalogy 61: 681–696.

______. 1988. Subspecies of pocket gophers: causal bases for geographic differentiation in *Thomomys bottae*. Systematic Zoology 37: 163–178.

SMITH, M. F., J. L. PATTON, J. C. HAFNER, AND D. J. HAFNER. 1983. *Thomomys bottae* pocket gophers of the central Rio Grande Valley, New Mexico: local differentiation, gene flow, and historical biogeography. Occasional Papers of the Museum of Southwestern Biology 2: 1–16.

SMITH, M. H., R. K. SELANDER, AND W. E. JOHNSON. 1973. Biochemical polymorphism and systematics in the genus *Peromyscus*. III. Variation in the Florida deer mouse (*Peromyscus floridanus*), a Pleistocene relict. Journal of Mammalogy 54: 1–13.

SNYDER, J. O. 1918. The fishes of the Lahontan system of Nevada and northeastern California. Bulletin of the United States Bureau of Fisheries 35: 33–86.

SUDMAN, P. D., J. R. CHOATE, AND E. G. ZIMMERMAN. 1987. Taxonomy of chromosomal races of *Geomys bursarius lutescens* Merriam. Journal of Mammalogy 68: 526–543.

SWOFFORD, D. L. 1981. On the utility of the distance Wagner procedure. Pages 25–43 *in* V. A. Funk and D. R. Brooks, eds., Advances in cladistics. Proceedings of the first meeting of the Willi Hennig Society, N.Y. Botanical Garden, Bronx, New York. xii + 250 pp.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS-1. A computer program for the analysis of allelic variation in genetics. Department of Genetics and Development, University of Illinois, Urbana.

TAYLOR, D. W. 1960. Distribution of the freshwater clam *Pisidium ultramontanum*: a zoogeographic inquiry. American Journal of Science, Bradley Vol. 258-A: 325–334.

THAELER, C. S., JR. 1973. The karyotype of *Thomomys townsendii similis* and comments on the karyotypes of *Thomomys*. Southwestern Naturalist 17: 327–331.

______. 1980. Chromosome numbers and systematic relations in the genus *Thomomys* (Rodentia: Geomyidae). Journal of Mammalogy 61: 414–422.

TUCKER, P. K., AND D. J. SCHMIDLY. 1981. Studies of a contact zone among three chromosomal races of *Geomys bursarius* in east Texas. Journal of Mammalogy 62: 258–272.

WELLS, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecological Monographs 53: 341–382.

WENTWORTH, F. A., AND D. A. SUTTON. 1969. Chromosomes of the Townsend pocket gopher, *Thomomys townsendii*. Southwestern Naturalist 14: 157–161.

WHEELER, H. E., AND E. F. COOK. 1954. Structural and stratigraphic significance of the Snake River capture, Idaho-Oregon. Journal of Geology 62: 525–536.

Whitlow, W. B., and E. R. Hall. 1933. Mammals of the Pocatello region of southern Idaho. University California Publications in Zoology 40: 235–276.

Wright, S. 1978. Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. University of Chicago Press, Chicago, Illinois. 580 pp.

Received 16 January 1990
Revised 15 January 1991
Accepted 20 February 1991

Appendix

Specimens Examined

Listed below are specimens used in electrophoretic and karyotypic analyses. Boldface numbers preceding localities represent corresponding composite locality numbers. Sample sizes in parentheses represent the number used for electrophoretic analysis and the number karyotyped, respectively.

Thomomys townsendii nevadensis

California: **Lassen Co., [30]**, Bird Flat Ranch, 3 mi. S, 2.7 mi. W Herlong, 4080 ft. (*n* = 27,5); **[31]**, 4 mi. W Standish, 4110 ft. (*n* = 18,2).

Nevada: **Elko Co., [10]**, 0.5 mi. SW Ryndon, 5100 ft. (*n* = 20,4); **Eureka Co., [11]**, Hay Ranch, 17 mi. SE Palisade, 5160 ft. (*n* = 19,3); **Humboldt Co., [5]**, Quinn River Crossing, 4100 ft. (*n* = 9,3); **Lander Co., [15]**, 5.5 mi. W Austin, 5700 ft. (*n* = 22,5); **Pershing Co., [3]**, Big Meadow Ranch, Lovelock, 4000 ft. (*n* = 16,3); **[1]**, 2 mi. NW Valmy, 4450 ft. (*n* = 21,5).

Oregon: **Harney Co., [4]**, 4 mi. SW Narrows, 4200 ft. (*n* = 6,0).

Thomomys townsendii townsendii

Idaho: **Bannock Co., [20]**, Floyd Johnson Ranch, 4 mi. NW Pocatello, 4500 ft. (*n* = 19,3); **Elmore Co., [22]**, 3 mi. E Grandview, 2800 ft. (*n* = 8,0); **Owyhee Co., [16]**, 7.5 mi. SE Grandview, 2600 ft. (*n* = 21,3); **[17]**, 6 mi. SE Murphy, 3000 ft. (*n* = 4,1); **Payette Co., [23]**, 1.5 mi. NE Payette, 2200 ft. (*n* = 9,1); **Power Co., [19]**, 2.5 mi. NW American Falls, 4500 ft. (*n* = 10,2); **Washington Co., [23]**, 2.9 mi. SE Weiser, 2100 ft. (*n* = 1,0).

Oregon: **Malheur Co., [24]**, 2.5 mi. N Ontario, 2100 ft. (*n* = 20,1).

Great Basin Naturalist 51(2), 1991, pp. 153–166

ECOLOGICAL RELATIONSHIPS OF CURLLEAF MOUNTAIN-MAHOGANY (*CERCOCARPUS LEDIFOLIUS* NUTT.) COMMUNITIES IN UTAH AND IMPLICATIONS FOR MANAGEMENT

James N. Davis[1] and Jack D. Brotherson[2]

ABSTRACT.—Curlleaf mountain-mahogany is a widely distributed shrubby tree of western North America. Well-developed stands are most often found on warm, dry, rocky ridges and slopes at high elevations on mostly southern exposures. It can, however, be found on all exposures. The species appears to be indifferent to substrate with soils which are invariably shallow and of low fertility. However, the nitrogen-fixing root nodules help overcome soil deficiencies. This highly palatable species is preferred by mountain sheep, mountain goats, deer, and elk. Its nutritive value (about 12% protein) and digestibility ratings (around 50%) in the winter are high when compared with most other associated winter browse species.

Early research with curlleaf mountain-mahogany basically dealt with two major management problems: (1) how to increase available forage production on old, even-aged stands too tall for big game to browse, and (2) how to increase reproduction in these same communities. Selective dozer thinning, sometimes in conjunction with the seeding of fast-growing plants, appears to be a promising management technique providing browse until the younger curlleaf becomes established.

Key words: Cercocarpus, *mountain-mahogany, habitat relationships, management.*

Curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) is a widely distributed shrubby tree of western North America, ranging from Helena, Montana, south to San Pedro Martin in Baja California, and from the Bighorn Mountains near Sheridan, Wyoming, to almost the West Coast in southwestern Oregon (Fig. 1). Its distribution is from 610 m to 1372 m in elevation in the northern and northwestern parts of its range and to 3000 m or more in the most southern parts of its range (USDA Forest Service 1937, Martin 1950). Duncan (1975) studied populations in Montana and found them to exist between 1200 m and 2100 m, with a mean of 1700 m.

Curlleaf mountain-mahogany is often associated with sagebrush, pinyon pine, juniper, scrub oak (mountain brush), ponderosa pine, and spruce-fir (Martin 1950). Tidestrom (1925) states that in central Nevada the species frequently takes the place of ponderosa pine and aspen at medium elevations, where it sometimes forms a noticeable transition community between pinyon and limber pine. Across the Great Basin, curlleaf mountain-mahogany actually occupies a narrow but unique position between the lower fringes of the conifer zone and the upper edges of the desert steppe. In California, but still within the Great Basin, Brayton and Mooney (1966) found curlleaf mountain-mahogany populations centered about 2000 m elevation in the subalpine zone. Here it occupied limestone, dolomite, sandstone, and granitic soils with a pH range of 6.5–8.4. Similar results were obtained in studies done by Miller (1964) in Wyoming and Scheldt (1969) in Idaho.

The best-developed stands of curlleaf mountain-mahogany are routinely found on warm, dry, rocky ridges or slopes at high elevations, primarily western or southern exposures (Tidestrom 1925, USDA Forest Service 1937, Martin 1950, Miller 1964, Brayton and Mooney 1966, Scheldt 1969, Thompson 1970, Duncan 1975). These stands are characteristically in isolated patches but infrequently will be found singularly or in continuous and extensive communities.

Taxonomic variability in the genus *Cercocarpus* has long been noted, and at present there are several opinions concerning its classification. Martin (1950) revised the genus *Cercocarpus* and delimited the *ledifolius*

---

[1] Utah Division of Wildlife Resources, Intermountain Research Station, Shrub Sciences Laboratory, 735 North 500 East, Provo, Utah 84606.

[2] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

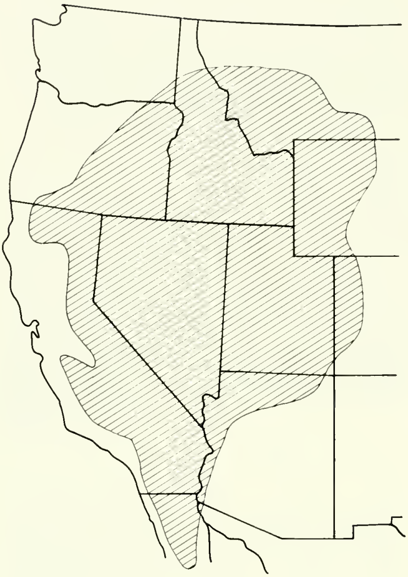


Fig. 1. Curlleaf-mahogany distribution.

lifeforms into three varieties. Others, however, have elevated these varieties into species rank (Tidestrom 1925, USDA Forest Service 1937, Martin 1950, Smith 1964, Brayton and Mooney 1966). Welsh et al. (1987) combined the varieties *typicus* and *intercedens* into *C. ledifolius*, while giving the variety *intricatus* separate species status. Holmgren (1987) determined that Nuttall's holotype for *C. ledifolius* was actually the more narrow-leafed taxon, while the more broad-leafed taxon had no name at any level. Therefore, Holmgren gave the more wide-leafed variety the name *C. ledifolius* var. *intermountainus.* Those interested in this taxonomic question can also refer to Stutz (1990). Because of the previous and confusing taxonomic treatments of *Cercocarpus ledifolius* by others, in this paper we do not distinguish between the two varieties of curlleaf mountain-mahogany. But the somewhat indistinct taxonomic interpretations can be summarized in the following manner. The narrow-leafed variety (*C. ledifolius* var. *ledifolius*) is widely distributed throughout the more northern and eastern portions of its distribution. The wide-leafed variety (*C. ledifolius* var. *intermountainus*) is commonly more central and southern in its distributional range, with both varieties found overlapping through the central portions of its range. The classification of Welsh et al. (1987) is followed in this paper, and any plant with elliptic leaves over 12 mm in length is considered to be *Cercocarpus ledifolius* Nutt.

Common names for *C. ledifolius* vary with location. Western pioneers called members of the genus mountain mahogany. The Federal Trade Commission, however, has since ruled that the name "mahogany" should not be used to designate any other genus except *Sweitenia*. The Forest Service checklist gives "Cercocarpus" as the common name of the genus (Hayes and Garrison 1960). But, several common names are still used when referring to *C. ledifolius* (i.e., desert mahogany, leatherleaf mahogany, and curlleaf mountain-mahogany).

Curlleaf mountain-mahogany is highly palatable to elk and deer (Smith 1950, Hoskins and Dalke 1955, Davis 1982). Because its nutritive value and digestibility ratings are high when compared with associated browse species, it merits attention in big game management (Smith 1952, 1957, Bissel and Strong 1955, Welch 1981). Welch and McArthur (1979) noted that curlleaf mountain-mahogany is one of only a few shrubs that exceed the protein requirements of wintering deer. Other authors also consider it an important winter forage plant (Tidestrom 1925, USDA Forest Service 1937, Liacos and Nord 1961, Scheldt 1969).

Dependence on curlleaf mountain-mahogany for winter forage can cause problems for wildlife because live branches are often beyond reach of browsing animals. Also, among populations in Utah, winter snows limit midwinter access to curlleaf mountain mahogany growing at high elevations. But, when curlleaf mountain-mahogany is available, it becomes an important forage species for mule deer and elk (Mitchell 1951, Smith 1952, Smith and Hubbard 1954, Richens 1967, Tueller 1979). Curlleaf mountain-mahogany has been noted as the third most important winter browse species for mule deer in northeastern Utah (Richens 1967) and also in eastern Oregon and

Washington (Mitchell 1951). It is especially essential for mountain goat survival in Idaho (Kuck 1980). In Utah, on one particularly critical mountain goat wintering area, it is the only browse available to about 80 animals (personal observation).

Most curlleaf mountain-mahogany investigative research has dealt with two major management problems: (1) how to increase available forage production on old, even-aged, out-of-reach curlleaf mountain-mahogany communities, and (2) how to increase reproduction in these same curlleaf mountain-mahogany communities.

In the late 1940s and early 1950s in Grant County, Oregon, different pruning techniques were tried as a means of improving forage production for wintering wildlife. Some of the methods showed promise, but most did not, and all were expensive (Lemons, n.d.).

Many other researchers have since investigated different pruning methods (Garrison 1953, Neff 1963, Thompson 1970, Shepherd 1971, Ormiston 1978, Austin and Urness 1980). Generally, clipping 50–75% or even as much as 98% of the limbs increased twig production the following year. In some cases rejuvenated twig production appeared to decrease after three or more years. The consensus was that pruning should be done during spring or early fall, and then mostly on the younger age classes. Pruning done during the winter, especially on older trees, caused death the next summer. Thompson (1970) noted that reproduction appeared to be better under individual trees that had been pruned. Pruning costs ran as high as $120/ha (Ormiston 1978).

Phillips (1970) prepared a summary of curlleaf mountain-mahogany rehabilitation projects on the Region 4 National Forests. The summary stated that in the 1960s the major problems in curlleaf communities were extensive highlining of older even-aged communities (which produced very little available browse) and little or no reproduction (Phillips 1970). Of special note was the bulldozing of strips parallel and perpendicular to the slope to decrease competition and allow young mahogany plants to become established. The treatment resulted in a spectacular increase in associated browse species that produced forage much faster and in greater quantities than did curlleaf mountain-mahogany. At the same time nearby older curlleaf mountain-mahogany provided excellent cover.

In a U.S. Forest Service report, Ferguson and Klemmedson (1965) examined most curlleaf mountain-mahogany ranges from southwestern Montana through southern Idaho. They found nearly all of the curlleaf communities in poor condition resulting from excessive use by wildlife and livestock. Personnel from the Forest Service and Montana Fish and Game Department stated that without curlleaf mountain-mahogany it would be almost impossible to maintain high populations of deer in the area of Beaverhead County, Montana. Again, the major problems observed were the failure of curlleaf to reproduce and the occurrence of edible browse beyond reach of browsing animals.

Winter forage areas are a major limiting factor for large deer populations in much of the Intermountain West. Available or suitable wintering areas are generally low in productivity, making their rehabilitation and management difficult. Current encroachment of human populations onto many of these winter ranges further complicates their management.

When it is desirable to maintain or increase game animal populations, the manager has but two alternatives: either to improve and/or to expand the winter range. Expanding the size of winter range is usually not feasible, but improvement can often be achieved. Successful improvement practices require an understanding of the structure and dynamics of the plant communities in question. In the case of curlleaf mountain-mahogany communities, such information is very limited. Additional ecological investigations are needed if managers are to more effectively manage this community type.

The authors' objective is to consolidate into one article information concerning the synecology of curlleaf mountain-mahogany communities gained through direct field studies along with correlated information from other authors of the last 20 or more years. Such a publication should permit better management and understanding of curlleaf communities and the big game populations that are totally or partially dependent on these communities for winter food and shelter.

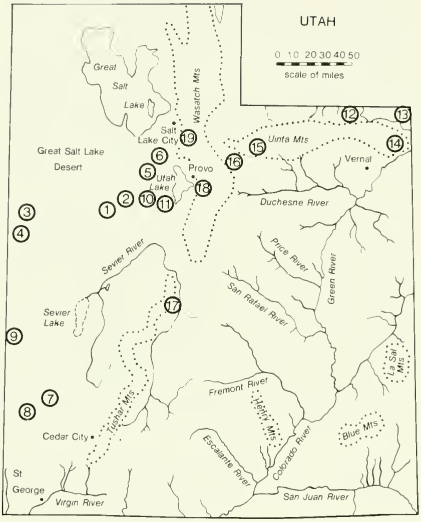

UTAH
0 10 20 30 40 50
scale of miles
Great Salt Lake
Wasatch Mts
Salt Lake City
Great Salt Lake Desert
Provo
Utah Lake
Uinta Mts
Vernal
Duchesne River
Sevier River
Price River
Green River
San Rafael River
Sevier Lake
La Sal Mts
Fremont River
Henry Mts
Tushar Mts
Blue Mts
Cedar City
Escalante River
Colorado River
St George
Virgin River
San Juan River
①
②
③
④
⑤
⑥
⑦
⑧
⑨
⑩
⑪
⑫
⑬
⑭
⑮
⑯
⑰
⑱
⑲

Fig. 2. Location of the 19 curlleaf mountain-mahogany study areas.

METHODS

Nineteen communities of curlleaf mountain-mahogany were selected for their large size and homogeneous nature (Fig. 2). Study plots of .04 ha were established within each community. Elevation, slope, and exposure for each plot were determined. Exposure values were transformed according to Beers et al. (1966), allowing the use of exposure as an independent variable in multiple regression analysis. Beers et al. (1966) used a northeast exposure for their optimum timber growth. However, according to our site quality index, curlleaf mountain-mahogany has its optimum growth on southwest exposures. Therefore we transformed the compass readings using the following equation:

$$\text{Southwest optimum} = \text{COS } (225 - \text{compass reading in degrees} + 1)$$

Twenty-five .25-m^2 quadrats in a 5 × 5 grid were equally spaced within the plot to help determine density, frequency, and cover of all plant species. Cover values were estimated as suggested by Daubenmire (1959). Trace species were recorded. A trace species was regarded as any plant species not occurring within any of the .25-m^2 quadrats but still occurring inside the study plot.

The most prevalent or important plant species were determined by multiplying constancy (in percentage) of each species (Oosting 1956) by average frequency (in percentage) in all stands (Curtis 1959).

A site quality index was based on stem diameter (measured 30 cm aboveground) divided by age and multiplied by 1,000. Stem diameter was used instead of tree height because of the dwarflike tree habit of curlleaf mountain-mahogany on many sites. Preliminary analyses demonstrated that stem diameter was better related to stem volume than was height in regression analyses.

All curlleaf mountain-mahogany plant heights within each .025-ha plot were measured to the nearest tenth of a meter. Stem basal diameter was recorded for each plant. The number of separate stems per tree was also determined at this same height.

Stand age for curlleaf mountain-mahogany was estimated by cutting five basal stems, one each (the largest if plants were multiple stemmed) from five different trees within the study plot. Stem diameter ranged from 2.5 to 20 cm. Even when sanded and stained, stems were difficult to age: annual rings are narrow and indistinct (Saul 1952, Dale 1968). Stems were independently counted at least twice to insure accuracy in estimates of age. Only stands 10 through 19 were aged. Ages of stands 1 through 9 were estimated using the following equation derived from stems taken from stands 10 through 19: age of tree = m (stem diameter) + B, where m = 17.8 (slope) and B = 11.2 (y intercept), R^2 = .67, which was significant (.01) for this equation.

Soil samples were taken at 5 of the 25 quadrats in each stand and were located at the corners and center of each study plot. Samples were taken to a depth of approximately 15 cm, and the 5 samples were combined for analysis. Samples were analyzed for texture, pH, and soluble salts. Soil depth, taken as the average of the 25 readings, was determined at each of the quadrats where soil samples were taken.

Similarities and differences in the vegetative parameters between the study sites were

TABLE 1. Physiographic characteristics of the curlleaf mountain-mahogany communities sampled in Utah.

Community characteristics	High	Low	Mean	Standard deviation
Elevation (m)	2725.00	2134.00	2397.60	172.80
Percent slope	81.00	18.00	45.40	15.90
Exposure[a]	1.98	.00	—	—
Soil depth (dm)	3.20	.60	1.64	.77
Percent sand	91.00	38.00	58.30	12.90
Percent silt	44.00	6.00	25.50	8.20
Percent clay	31.00	3.00	16.20	61.00
Soil pH	7.80	5.90	6.90	.60
Soil soluble salts (ppm)	550.00	92.00	278.30	113.00

[a] Numbers relate to Beers et al. (1966) transformations (2.00 equals Southwest).

calculated using Sorenson's index of similarity (Sorenson 1948, Dix and Butler 1960).

Cluster analysis techniques (Sneath and Sokal 1973) were applied to the interstand similarity values. In this way, interstand compositional similarities were graphically represented. Multiple stepwise regression and correlation analyses were made using standard programs available at Brigham Young University.

RESULTS AND DISCUSSION

Physiographic Characteristics

Physiographic characteristics of the curlleaf mountain-mahogany communities examined in this study are reported in Table 1. Elevation ranged from 2134 m to 2725 m and averaged 2398 m.

Curlleaf mountain-mahogany appears to occur at a higher average elevation in Utah, Nevada, and east central California than anywhere else in its range. Stands of the species, while occurring below 2134 m in Utah, are rarely large enough to accommodate study plots of the size employed in this study. Extensive stands were observed above 3050 m in the Deep Creek Mountains of western Utah, but they were not sampled. Brayton and Mooney (1966) found curlleaf mountain-mahogany communities centered at elevations just above 2800 m in the White Mountains of east central California. Such high-elevation stands are not unusual on the higher southern mountain regions of the Great Basin. Lewis (1971) reports well-developed curlleaf mountain-mahogany communities occurring from 2230 to 2787 m in the Ruby Mountains of northeastern Nevada.

In Montana, Duncan (1975) reports that curlleaf mountain-mahogany forms a distinct community type over an elevational range of 1165–2152 m. Miller (1964) in Wyoming and Scheldt (1969) in Idaho found very similar elevational ranges. Dealy (1975) found curlleaf mountain-mahogany ranging from 1375 to 2271 m in the area of southeastern Oregon. Lower altitude preferences for the species near its northern range limit are to be expected.

Well-developed stands are usually found on steeply sloping land; slopes averaged 45% in Utah. Miller in Wyoming (1964), Scheldt in Idaho (1969), and Duncan in Montana (1975) had similar average slopes of 48, 53, and 48%, respectively. Sampled stands occurred on all exposures, as was also reported by Miller (1964), Brayton and Mooney (1966), Scheldt (1969), Dealy (1975), and Duncan (1975). Although occurring on all exposures, curlleaf mountain-mahogany appears most commonly on south and southwest exposures.

True mountain-mahogany (*Cercocarpus montanus* Raf.) communities in Utah are reported by Anderson (1974) to range from 1511 to 2195 m. Generally then, the altitudinal ranges of curlleaf mountain-mahogany and true mountain-mahogany overlap little in Utah. These congeners exhibit little difference, however, with respect to slope steepness and exposure preferences.

Edaphic Characteristics

Soils underlying the curlleaf mountain-mahogany communities studied were invariably shallow, with an average penetrometer depth of 1.65 dm. This corresponds closely to results of studies by Miller (1964) and Duncan (1975). The soils are commonly sandy loams; however, a few stands occurred on loam, clay loam, and sandy loam sites. Soil reaction tended to be circumneutral (modal pH of 7.1), but individual stands were observed on sites as acidic as 5.9 and as basic as 7.8. Miller (1964) and Duncan (1975) noted a pH of 7.6 and 7.5 in Wyoming and Montana, respectively. Soluble salts were low in all the soils analyzed, with a range of 92–550 ppm. These figures correspond to the findings of Miller (1964), Brayton and Mooney (1966), Scheldt (1969), and Duncan (1975). Brayton and Mooney (1966) also reported occurrences of this species in California on shallow soils of low fertility where it appeared to be indifferent to substrate. Duncan (1975) found the species on soils in Montana that were very low in phosphorus and only intermediate in respect to potassium.

Youngberg and Hu (1972) reported in an Oregon study that curlleaf mountain-mahogany produces root nodules capable of fixing nitrogen. They also discovered that foliage from nodulated plants has the highest amounts of nitrogen. Lepper and Fleschner (1977) found that soils supporting limber pine–curlleaf mountain-mahogany stands have higher percentages of total nitrogen than soils beneath similar limber pine stands without the curlleaf mountain-mahogany association. They concluded that the ability to fix nitrogen is a frequent occurrence in extreme or pioneer habitats.

If the capacity to fix nitrogen is universal in curlleaf mountain-mahogany, it would help to explain how the species can successfully occupy the infertile sites that it regularly colonizes.

In respect to soil preferences, curlleaf mountain-mahogany and true mountain mahogany diverge widely in Utah. Anderson (1974) found the most common textural class for the latter species to be clay loam. Soil depths were almost twice as great in true mountain mahogany stands (Anderson 1974) as in the curlleaf stands reported here. Further, this study also indicates that curlleaf mountain-mahogany occurs on less basic and less saline soils than does true mountain mahogany.

Synecological Characteristics

Vegetative parameters for curlleaf mountain-mahogany communities are listed in Tables 2, 3, and 4. Canopy coverage values varied from 20% to as high as 63%, with a mean of 40%. The mean canopy height per site varied from 2.0 to 4.6 m, with an average of 3.4 m for all sites combined. Curlleaf mountain-mahogany densities ranged from a high of 417 plants per ha to a low of 60.7 plants per ha, with a mean of 171.1 per ha.

In Montana, curlleaf mountain-mahogany densities were much greater than those observed in this study. Densities varied from 472 to 21,627 individuals per ha, with a mean of 3,397 per ha (Duncan 1975). Scheldt (1969), in Idaho, showed a mean of 511 trees per ha.

Data on other variables obtained during the sampling were analyzed using multiple regression. These entities, along with their influencing factors and their coefficients of determination, are listed in Table 5. Those with 50% or more of the variation accounted for were: mean canopy cover ($R^2 = .74$), mean canopy height ($R^2 = .64$), relative percent frequency of shrubs per stand ($R^2 = .58$), relative percent frequency of biennial forbs per stand, ($R^2 = .66$), and relative percent frequency of *Carex* species per stand ($R^2 = .55$). Mean canopy cover per stand appeared to be most affected by moisture-related factors because slope, exposure, and percent sand within the soil together accounted for 64% of the .74 R^2 value. Mean height per stand was most affected by soil pH ($R^2 = .12$) and soluble salts ($R^2 = .40$). Curlleaf mountain-mahogany density appeared not to be affected ($R^2 = .34$) by moisture-related factors.

The most important or prevalent species on the curlleaf mountain-mahogany study sites are listed in order of importance in Table 4. The 23 prevalent species of this study account for only 16% of the 148 species encountered in the study. But, they contribute more than 90% of the living cover in an average stand. The prevalent species are predominantly perennial (91%). More than 80% of the living cover (Table 3) in an average stand is contributed by woody or suffrutescent species. Perennial grasses account for only 7% of the cover. Perennial dicotyledonous herbs and annuals account for the remainder, with perennials furnishing about twice as much cover as annuals (Table 3). The large contribution of woody plants and perennial grasses in the community is probably related to the xeric nature of the sites dominated by curlleaf mountain-mahogany (Harner and Harper 1973, Yake and Brotherson 1979). The dominance

TABLE 2. Curlleaf mountain mahogany stand characteristics determined from the 19 stands studied in Utah.

Curlleaf mahogany characteristics	High	Low	Mean	Standard deviation
Trees/ha	417.00	60.00	171.30	81.90
Percent canopy cover	63.30	19.60	40.00	13.40
Mean canopy height (m)	4.70	2.10	3.40	.80
Mean stem diameter (cm)	18.50	5.10	10.40	3.20
Mean stems/tree	5.60	1.70	3.40	1.20
Seedlings/0.025 ha	23.00	.00	3.70	7.10
Mean age/site	142.92	47.51	85.47	23.09
Site quality index	772.00	290.00	486.30	93.20

TABLE 3. Vegetational characteristics of curlleaf mountain-mahogany communities studied in Utah.

Vegetational characteristics	High	Low	Mean	Standard deviation
Species/stand	37.00	15.00	22.90	5.80
Species/quadrat (mean)	5.40	1.60	3.70	1.20
Percent understory cover	70.00	7.00	33.40	15.90
Percent canopy cover	93.00	30.00	66.60	15.90
Percent shrub cover	55.00	1.00	17.30	13.40
Percent perennial grass	35.00	1.00	7.20	8.70
Percent perennial forb	22.00	1.00	5.90	5.90
Percent annual cover	27.00	.00	3.20	6.20
Percent sedge cover	1.00	.00	.20	.40

TABLE 4. Prevalent plant species of Utah curlleaf mountain-mahogany communities. Species are arranged in decreasing order of average importance in the community.

Species	Life-form	Percent constancy (a)	Mean percent frequency per stand (b)	Prevalent index (a × b)
Cercocarpus ledifolius	tree	100	69.89	6989
Symphoricarpos oreophilus	shrub	89	20.63	1836
Agropyron spicatum	grass	79	16.63	1314
Berberis repens	shrub	74	14.74	1091
Artemisia tridentata	shrub	74	6.74	499
Bromus tectorum	annual grass	47	9.47	445
Arenaria kingii	subshrub	42	10.53	442
Poa fendleriana	grass	37	6.95	257
Amelanchier utahensis	shrub	53	4.84	257
Oryzopsis hymenoides	grass	47	4.84	227
Erigeron spp.	shrub	37	6.11	226
Pachistima myrsinites	shrub	26	7.37	192
Chrysothamnus viscidiflorus	shrub	47	4.00	188
Penstemon spp.	forb	32	5.47	175
Hesperochloa kingii	grass	32	5.05	162
Quercus gambelii	shrub	32	4.63	148
Collinsia parviflora	annual forb	21	6.68	140
Poa secunda	grass	21	5.89	124
Stellaria jamesiana	forb	16	7.05	113
Pinus monophylla	tree	37	2.95	109
Festuca ovina	grass	21	4.00	84
Eriogonum microthecum	shrub	26	3.16	82
Agropyron trachycaulum	grass	21	3.58	75

Table 5. Results of multiple regression analysis (R^2) on measured characteristics of curlleaf mountain-mahogany communities.

	Measured community environmental characters										
Dependent variables	Slope	Exposure	Elevation	Soil depth	Soil pH	% sand	% fines	% silt	% clay	Soluble salts	Coef. of determ.
Curlleaf mountain-mahogany											
Mean cover/stand	−.35	−.07		−.06	−.04	−.22					.74
Mean height/stand	−.05			−.07	−.12					.40	.64
Mean stems/tree	.03	−.01	.02			.08				−.52	.66
Subbasal area/stand	−.13	.22	.18		.10						.63
Site index (diameter/age)		.04	.34		−.05		.01			.30	.74
Mean species/quadrat	−.01		.04	.24							.29
Sum % cover for all species/stand			.06	.05	.05		.34			.04	.54
Sum % cover shrubs/stand		−.18			.23		.01				.42
% relative freq. trees	.04	.07		−.15	−.01			.05	.06		.38
% relative freq. shrubs		−.14	.07		.05		.06			.25	.58
% relative freq. peren. forbs	−.03		.27	.22			−.03			.05	.60
% relative freq. biennial forbs	−.03			.15	.03		−.45				.66
% relative freq. annual forbs	−.02	.08					.03			−.14	.27
% relative freq. perennial grass				.04			.17				.21
% relative freq. annual grass		.10	−.07	.10			.06			−.02	.35
% relative freq. *Carex* spp.	−.10		.04				−.39			.02	.55

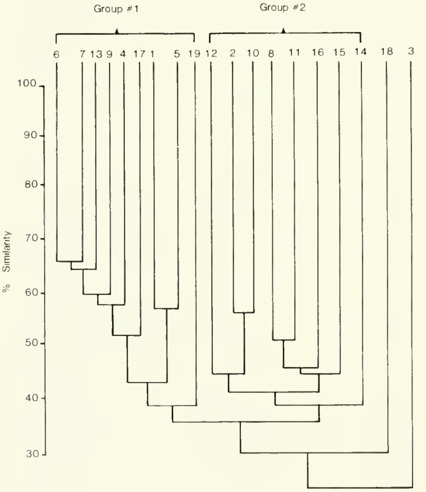


Fig. 3. Clustering of the 19 curlleaf mountain-mahogany study areas based on cover composition and 40% similarity.

and variety of woody species in the community help to insure that forage of good variety and quality will remain exposed to game animals even with considerable snowcover on the ground. Curlleaf mountain-mahogany stands on south and southwest exposures are known to attract concentrations of big game animals during early and late winter or throughout a mild winter in Utah.

Clustering techniques (Sneath and Sokal 1973) based on cover composition of the vegetation show two major groups clustering above the 40% similarity level (Fig. 3). One group (designated 1) contains eight stands, and the other group (designated 2) contains seven stands. An unpaired *t* test was used to test for significant differences in vegetative and environmental characteristics between the two cluster groups. Results indicated that curlleaf mountain-mahogany canopy cover, percent of soil fines (clay and silt), and percent of sand were the only measured variables that exhibited significant differences with respect to the two groups.

To determine which environmental variables exerted the most influence on curlleaf mountain-mahogany performance, the site quality index was correlated via multiple stepwise regression with values for several environmental variables. The analysis showed that elevation, soluble salts, exposure, soil pH, and percent of fines together accounted for 74% of the variation in performance of curlleaf mountain-mahogany in the stands sampled. Of this variation, 85% of the total is accounted for by elevation and soluble salts (Table 5).

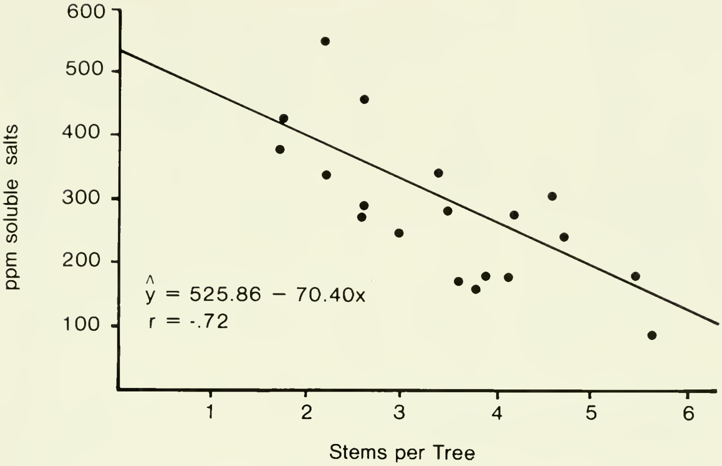


Fig. 4. Regression plot showing relationship between curlleaf mountain-mahogany branching habit and soluble salts.

The equation for this relationship is: site quality = $0.56x_1 + 0.09x_2 + 3.2x_3 - 48.5x_4 + 0.66x_5 - 156.6$ (x_1 = elevation, x_2 = soluble salts, x_3 = exposure, x_4 = pH, x_5 = percent fines).

Although the site quality index identifies those sites where the species grows most rapidly, it is poorly correlated with available browse for big game because the "highest quality sites" in this study characteristically produced curlleaf individuals that are more treelike than shrublike in habit.

Growth Form

Curlleaf mountain-mahogany growth habit varied from treelike (1.75 stems per tree) to shrublike (5.6 stems per tree). Varying growth forms were also observed in Idaho (Scheldt 1969), Wyoming (Miller 1964), and Montana (Duncan 1975). Stem diameter per tree ranged from 5.0 cm to 18.5 cm, with an average of 10.6 cm (4.1 in). Regression analysis revealed that the branching habit of curlleaf mountain-mahogany in Utah is significantly correlated with soluble salts and percent of sand in the soil (Figs. 4, 5). This relationship could be important when considering establishment of curlleaf mountain-mahogany onto new areas. Knowing the amount of sand and soluble salts may allow one to estimate whether or not the plants would develop shrub- or treelike habits. The effect of soluble salts and sand content on the mean number of stems per tree is made even more evident in multiple stepwise regression. Soluble salts alone accounted for 52% of the total 66% variation, or 79% of the total variation accounted for by the regression (Table 5). Without common garden studies, one cannot determine whether this branching habit is an environmentally adaptive response or a fixed genetic response.

The average canopy height per site in this study varied from 2.0 to 4.6 m, with a mean of 3.4 m. This may be misleading, for many trees were observed to be over 6 m tall on some of the sites studied. For example, site 9 near Baker Lake Trail in the Humboldt National Forest had trees over 9 m tall. Scheldt (1969) found the average height to be 2.9 m in his Idaho study. In contrast, Duncan (1975) found that sites in Montana west of the Continental Divide had an average canopy height of 1.7 m, while sites east of the Divide had an average canopy height of only 0.9 m.

Age and Reproduction

Mean ages for curlleaf stems on the 19 study sites ranged from 48 to 143 years, with an average age for all study sites of 85 years.

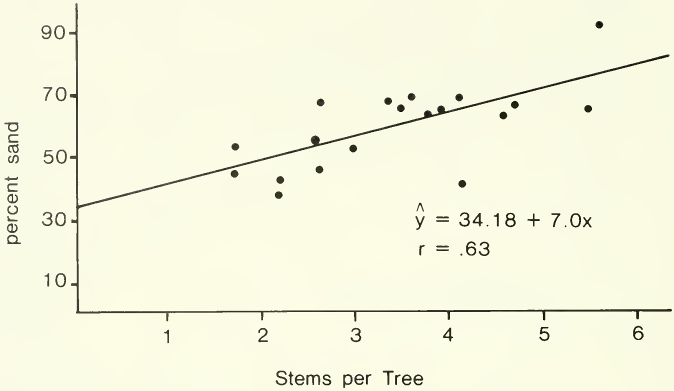


Fig. 5. Regression plot showing relationship between curlleaf mountain-mahogany branching habit and percent sand.

Age distributions (Fig. 6) indicate that 58% of the individuals sampled fall between the ages of 56 and 109 years.

Dealy (1975) rarely encountered trees larger than 25 cm in diameter in Oregon. Over 90% of all trees sampled in his study were less than 20 cm in diameter. In this study, 74% of the trees had diameters 15 cm or less, while 26% were over 15 cm in diameter (109 years of age or older). Thus, Utah stands appear to be older in average age than the Oregon stands. These comparisons can be made between Oregon and Utah because a line midway between Dealy's (1975) two regression lines, one for dry sites and one for moist sites, would estimate a 20.3-cm stem to be 130 years old. Using the diameter-age regression equation developed in this study, one could estimate the age of the same 20.3-cm stem to be 131 years. Such remarkable similarity between regression equations would suggest that curlleaf mountain-mahogany growth is similar between Oregon and Utah.

Forty-seven percent of the areas sampled had no trees in the size class less than 2.5-cm (20-year age class) (Fig. 6), indicating little or no reproduction on these sites. This could be due to shade intolerance of curlleaf mountain-mahogany seedlings, competition for water and mineral nutrients with adult curlleaf mountain-mahogany and other understory species, autotoxicity of litter to seedings of the species, or overutilization by wildlife. Such low rates of reproduction in a species whose individuals are capable of living to be well over 723 years (estimated age of 100-cm-diameter stem near site 17) may not, however, be a serious deficiency. Individuals of great longevity should be able to find ample opportunity to replace themselves over an extended period.

Ages reported for curlleaf mountain-mahogany in the Montana study (Duncan 1975) were much younger than those for Utah or Oregon. Trees in sites west of the Continental Divide had a mean age of 31 years, with a range of 5 to 85 years. Trees on sites east of the Divide were still younger, with a mean age of only 20 years. Eight percent of the individual samples were classified as young, mean age 10.8 years. Sixty-two percent were classified as mature, mean age 39.5 years. Thirty percent were classified as decadent, mean age 49.9 years.

In this study about 10% of the individuals were considered decadent. Mean age of decadent (more than 25% of the crown was dead) individuals in Utah was about 167 years. This lower percentage of decadence may possibly be attributable to the difference in plant height: taller trees would not suffer as much browsing damage as would the shorter Montana plants. The oldest tree recorded in Duncan's (1975) study was 130 years. The oldest stands we are aware of are from central and

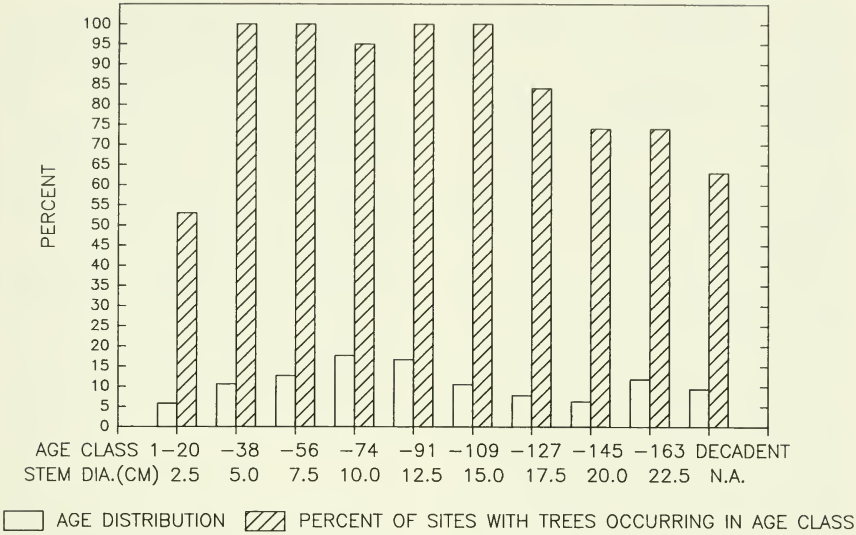


Fig. 6. Curlleaf mountain-mahogany distribution of stem-diameter classes and their associated age for the 19 stands sampled.

western Nevada; ages range from 134 to 482 years with a mean of 352 years (Schultz et al. 1990).

Once germination has taken place, the seedlings appear to be well adapted for establishment in xeric habitat. Dealy (1975) reported that curlleaf seedings had a mean taproot length of 0.97 m after 120 days. The mean top height for the seedlings after 120 days was slightly less than 2.5 cm, with a mean leaf area of 4 cm^2/seedling.

Reproduction on all study sites was generally poor, ranging from no seedings (in 47% of the study plots) to 568 seedlings per ha in plot 13. The average number of seedlings per plot was 222 per ha. Duncan (1975) reported an average of 134 seedlings per ha, with a range of 0 to 660 seedlings per ha in Montana. Sixty-eight percent of her study areas had no seedlings. The great variation in reproduction would indicate that a critical combination of environmental conditions must exist for germination and seedling establishment. Scheldt and Tisdale (1970) and Dealy (1975) also observed that insect predation on mature seeds is a common occurrence. Good seed crops occur only every 2 to 10 years according to Plummer et al. (1968). Variations in seed production from year to year could be one explanation for poor reproduction. Dealy (1975) found that no special chemical treatment was needed for germination of the seeds other than being stratified in a moist medium at 4 C over a 220-day period. He obtained 88% germination after such treatment. This suggests that a wet, somewhat mild winter is required for good stratification and that an unusually wet spring-summer is needed for good seedling germination and establishment.

Scheldt and Tisdale's (1970) counts of seedling survival through the first summer revealed that most mortality was due to drought. Winter mortality, also high, was due to grazing, mostly thought to be rabbits. The lack through time of proper combinations of critical parameters needed for germination and growth of young curlleaf mountain-mahogany plants may help to explain why reproduction is so poor on most curlleaf mountain-mahogany sites.

MANAGEMENT IMPLICATIONS

The management of curlleaf mountain-mahogany is difficult because the species does not resprout after burning or chaining and is very troublesome to establish from seed. These characteristics do not leave many options for management manipulation. The major problem confronting the manager will be, What do you do with old, decadent communities of curlleaf with out-of-reach browse? There are no feasible quick-fix methods for this problem. The pruning studies are examples of feasible but basically impractical treatments for increasing production. The best overall approach to this problem, in the long term, would be to thin or take out old trees in small, randomly placed and shaped openings. This would allow associated shrub species to be released while allowing openings for curlleaf seedlings to become established. The thinning process could be done by selective dozing or chaining, depending on the size and shape of the openings wanted within a stand. Release of associated species would give some immediate relief with respect to overuse of the curlleaf mountain-mahogany and also allow younger age classes of curlleaf mountain-mahogany time to become available. Some communities of curlleaf may lack associated browse species; here selective removal would probably only promote establishment of young seedlings. If other browse species are wanted, especially species that grow more rapidly, seed dribblers (placed over both bulldozer tracks) could be used to plant species that would provide browse much sooner than the slow-growing curlleaf. But, such species should not be planted in densities so high as to hamper curlleaf establishment; curlleaf seedlings are not strongly competitive. This close association could also be of benefit because curlleaf mountain-mahogany has soil-enriching attributes as noted by Lepper and Fleschner (1977).

Curlleaf mountain-mahogany communities appear to be stable or "climax" in nature. Rates of succession are considered to be extremely slow and dependent upon habitat factors relating to storage of soil moisture and to soil development processes, which are also slow in these xeric environments. On site 17, however, white fir had a cover value of 40%. The white fir trees were taller than curlleaf mountain-mahogany (site 17 average height 4.7 m [15.5 ft]), but with time the white fir will likely shade out the shorter curlleaf mountain-mahogany plants. Another problem would be snow loads falling from the white fir trees and breaking limbs in the shorter and less flexible curlleaf mountain-mahogany. Because white fir occurred on only 2 of the 19 sites sampled, displacement of curlleaf mountain-mahogany by white fir is not thought to be a common occurrence in Utah. Site 17 was the only area sampled that had clay-loam soil, which may account for the response of fir there.

Dealy (1975) thought that the survival of curlleaf mountain-mahogany communities was dependent on fire-resistant rocky sites. Trees on such sites were larger and older than those on nearby nonrocky sites. These trees also provided seed if fire destroyed the nonrocky portion of the community. Dealy's opinion was based on finding charred trees and charcoal bits on nonrocky study areas. Scheldt (1969) observed similar patterns in areas in southern Idaho. We also observed that the larger trees occurred on the most rocky areas; the younger trees occurred on nearby areas of gentler slope and less rocky soils. We found no evidence of fire, however, on any of the study sites in Utah.

The fact that curlleaf mountain-mahogany produces good seed crops at very irregular intervals and is difficult to establish because its seedlings are sensitive to drought and frost (Plummer et al. 1968, Dealy 1975) may explain its common stand characteristics. Once a few trees are established, the "pioneering" individuals usually grow to large size before conditions for germination and growth of seedlings are met. Moreover, seedlings must compete with other established plant species. Rocky sites would offer less competition during establishment.

The distribution of curlleaf mountain-mahogany communities is not expected to change significantly in the future. The community type appears to be physiologically and morphologically adapted to a narrow elevation and/or moisture range of about 2000–3000 m in Utah. At higher elevations the exclusion of *C. ledifolius* from most areas is likely determined by competition with conifers and other plant species, which are more competitive for sunlight and moisture. Curlleaf mountain-mahogany can avoid competition by growing on ridges, canyon ledges, or high plateaus with poor soil development where the conifers do not establish well. The lower altitudinal distribution patterns are most likely determined by lack of competitive ability on sites where soils are deeper and where mountain brush and pinyon-juniper do well.

Curlleaf mountain-mahogany communities are important because they grow in habitats where few other desirable woody plants will, and thus they provide plant cover for stabilizing otherwise unstable systems. Also, in their young stages these communities provide valuable forage for big game; later, as the communities age, they supply much-needed shelter in winter where environmental extremes predominate. More information is needed on ecological significance of curlleaf mountain-mahogany's soil-enriching attributes and possible effects on associated plant species.

ACKNOWLEDGMENTS

Funds were provided through Federal Aid for Wildlife Restoration, Project W-82-R, Jobs 1 and 5, U.S. Department of Agriculture, Intermountain Research Station, Forest Service. We also thank Robert Ferguson, Kimball Harper, Durant McArthur, and Edward Dealy for their helpful reviews of the manuscript.

LITERATURE CITED

ANDERSON, D. L. 1974. Ecological aspects of *Cercocarpus montanus* Raf. communities in central Utah. Unpublished thesis, Brigham Young University, Provo, Utah.

AUSTIN, D. D., AND P. J. URNESS. 1980. Response of curlleaf mountain-mahogany to pruning treatments in northern Utah. Journal of Range Management 33: 275–277.

BEERS, T. W., P. E. DRESS, AND L. C. WENSEL. 1966. Aspect transformation in site productivity research. Journal of Forestry 64: 691.

BISSELL, H. D., AND H. STRONG. 1955. The crude protein variations in the browse diet of California deer. California Fish and Game 41: 145–155.

BRAYTON, R., AND H. A. MOONEY. 1966. Population variability of *Cercocarpus* in the White Mountains of California as related to habitat. Evolution 20: 383–391.

CURTIS, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison.

DALE, A. 1968. Comparative wood anatomy of some shrubs native to the northern Rocky Mountains. USDA Forest Service Research Paper INT-45, pp. 12–13. Intermountain Forest and Range Experiment Station, Ogden, Utah.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33: 43–46.

DAVIS, J. N. 1982. Unpublished data on file at the Shrub Sciences Laboratory, 735 N. 500 E., Provo, Utah.

DEALY, E. J. 1975. Ecology of curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) in eastern Oregon and adjacent areas. Unpublished dissertation, Oregon State University, Corvallis.

DIX, R. L., AND J. E. BUTLER. 1960. A phytosociological study of a small prairie in Wisconsin. Ecology 41: 316–327.

DUNCAN, E. 1975. The ecology of curlleaf mountain-mahogany in southwestern Montana with special reference to use by mule deer. Unpublished thesis, Montana State University, Bozeman.

FERGUSON, R. B., AND J. O. KLEMMEDSON. 1965. Reconnaissance of *Cercocarpus ledifolius* winter range in southern Idaho and southwestern Montana. USDA Forest Service, 26 May 1965, Ogden, Utah. [Mimeo.]

GARRISON, G. A. 1953. Effects of clipping on some range shrubs. Journal of Range Management 6: 309–317.

HARNER, R. F., AND K. T. HARPER. 1973. Mineral composition of grassland species of the eastern Great Basin in relation to stand productivity. Canadian Journal of Botany 51: 2037–2046.

HAYES, D. W., AND G. A. GARRISON. 1960. Key to important woody plants of eastern Oregon and Washington. USDA Handbook 148.

HOLMGREN, N. H. 1987. *Cercocarpus ledifolius* var. *intermountanus* (Rosaceae), a new varietal name for the Intermountain curlleaf mountain-mahogany. Brittonia 39: 423–427.

HOSKINS, L. W., AND P. D. DALKE. 1955. Winter browse on the Pocatello big game winter range in southeastern Idaho. Journal of Wildlife Management 19: 215–225.

KUCK, L. 1980. Ghost of the crags. Idaho Wildlife 2: 16–22.

LEMONS, C. n.d. Mahogany stand improvement projects on deer winter range. Oregon State Game Commission. [Mimeo.]

LEPPER, M. G., AND M. FLESCHNER. 1977. Nitrogen fixation by *Cercocarpus ledifolius* (Rosaceae) in pioneer habitats. Oecologia (Berlin) 27: 333–338.

LEWIS, M. E. 1971. Flora and major plant communities of the Ruby–East Humboldt Mountains. Mimeographed report of the Humboldt National Forest, USDA Forest Service.

LIACOS, L. G., AND Z. C. NORD. 1961. Curlleaf *Cercocarpus* seed dormancy yields to acid and thiorea. Journal of Range Management 14: 317–320.

MARTIN, F. L. 1950. A revision of *Cercocarpus*. Brittonia 7: 91–111.

MILLER, W. B. 1964. An ecological study of the mountain mahogany community and related biotic associations of the Big Horn Mountains. Unpublished thesis, University of Wyoming, Laramie.

MITCHELL, G. F. 1951. Status of browse on ranges of eastern Oregon and eastern Washington. Journal of Range Management 4: 249–253.

NEFF, D. J. 1963. The effects of clipping on the vigor of big game browse plants and related studies in the Arizona chaparral. Unpublished dissertation, Oregon State University, Corvallis.

OOSTING, H J. 1956. The study of plant communities. W. H. Freeman and Co., San Francisco, California.

ORMISTON, J. H. 1978. Response of curlleaf mountain-mahogany to top pruning in southwest Montana. Pages 401–402 *in* Proceedings of First Intermountain Rangeland Congress, Denver, Colorado.

PHILLIPS, T. 1970. Summary report of curlleaf mahogany rehabilitation projects in Region 4. USDA Forest Service, Ogden, Utah. [Mimeo.]

PLUMMER, A. P., D. R. CHRISTENSEN, AND S. B. MONSEN. 1968. Restoring big-game range in Utah. Utah Division of Fish and Game Publication No. 683.

RICHENS, V. V. 1967. Characteristics of mule deer herds and their range in northeastern Utah. Journal of Wildlife Management 31: 651–666.

SAUL, W. E. 1952. The identification of woody shrubs of Utah based on stem anatomy. Unpublished thesis, University of Utah, Salt Lake City.

SCHELDT, R. S. 1969. Ecology and utilization of curlleaf mountain-mahogany in Idaho. Unpublished thesis, University of Idaho, Moscow.

SCHELDT, R. S., AND E. W. TISDALE. 1970. Ecology and utilization of curlleaf mountain-mahogany in Idaho. University of Idaho, College of Forestry, Wildlife and Range Science, Moscow. Station Note No. 15.

SCHULTZ, B. W., P. T. TUELLER, AND R. J. TAUSCH. 1990. Ecology of curlleaf mountain-mahogany (*Cerocarpus ledifolius*) in western and central Nevada: I. Community and population structure. Journal of Range Management 43: 13–20.

SHEPHERD, H. R. 1971. Effects of clipping on key browse species in southwestern Colorado. Colorado Division of Game, Fish and Parks Technical Publication No. 28.

SMITH, A. D. 1950. Feeding deer on browse species during winter. Journal of Range Management 3: 130–132.

______. 1952. Digestibility of some native forages for mule deer. Journal of Wildlife Management 16: 309–312.

______. 1957. Nutritive value of some browse plants in winter. Journal of Range Management 10: 162–164.

______. 1964. Evidence of hybridization between certain browse plants. Journal of Range Management 17: 269–272.

SMITH, A. D., AND R. L. HUBBARD. 1954. Preference ratings for winter deer forages from northern Utah ranges based on browsing time and forage consumed. Journal of Range Management 7: 262–265.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco.

SORENSON, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Knoge Dean Vidensk, Selsk., JS 4: 1–34.

STUTZ, H. 1990. Taxonomy and evolution of *Cercocarpus* in the western United States. *In* K. L. Johnson, ed., Proceedings of Fifth Utah Shrub Ecology Workshop, Utah State University, Logan. 104 pp.

TIDESTROM, I. 1925. Flora of Utah and Nevada. U.S. National Herbarium. Vol. 25. Smithsonian Institute. 665 pp.

THOMPSON, R. M. 1970. Experimental top pruning of curlleaf mountain-mahogany trees on the South Horn Mountain, Ferron Ranger District, Manti-LaSal National Forest, USDA Forest Service Range Improvement Notes, Vol. 15, No. 3.

TUELLER, P. T. 1979. Food habits and nutrition of mule deer on Nevada ranges. Agricultural Experiment Station, University of Nevada, Reno.

USDA FOREST SERVICE. 1937. Range plant handbook. U.S. Department of Agriculture, Washington, D.C.: U.S. Government Printing Office.

WELCH, B. L. 1981. Nutritive value of big sagebrush and other shrubs. Pages 9–22 *in* Lavern H. Stelter, Edward J. Depuit, and Sharon A. Mikol, eds., Proceedings, Shrub Establishment on Disturbed Arid and Semi-arid Lands, Wyoming Game and Fish Department.

WELCH, B. L., AND E. D. MCARTHUR. 1979. Feasibility of improving big sagebrush (*Artemisia tridentata*) for use on mule deer winter ranges. Pages 451–473 *in* J. R. Gooding and D. K. Northington eds., Proceedings of Arid Land Plant Resources, Intermountain Center for Arid and Semi-arid Land Studies, Texas Tech. University, Lubbock.

WELSH, S. L., N. D. ATWOOD, L. C. HIGGINS, AND S. GOODRICH. 1987. A Utah flora. Great Basin Naturalist Memoirs No. 9. 894 pp.

YAKE, S., AND J. D. BROTHERSON. 1979. Differentiation of serviceberry habitats in the Wasatch Mountains of Utah. Journal of Range Management 32: 379–383.

YOUNGBERG, C. T., AND L. HU. 1972. Root nodules on mountain mahogany. Forest Science 18: 211–212.

Received 1 May 1990
Revised 8 January 1991
Accepted 27 February 1991

Great Basin Naturalist 51(2), 1991, pp. 167–175

SITE CHARACTERISTICS AND HABITAT REQUIREMENTS OF THE ENDANGERED DWARF BEAR-CLAW POPPY (*ARCTOMECON HUMILIS* COVILLE, PAPAVERACEAE)

Deanna R. Nelson[1] and Kimball T. Harper[1]

ABSTRACT.—*Arctomecon humilis* Cov. is a narrow endemic, confined to gypsiferous substrates derived from the Shnabkaib Member of the Moenkopi Formation in southwestern Utah. The characteristics of seven *A. humilis* sites were studied to define habitat requirements of the species. Both physical and biotic aspects of the habitat were analyzed; geology, soil chemistry, and physical properties, as well as vascular and nonvascular plant communities, were studied. Chemical and physical properties of these soils vary considerably from those supporting adjacent desert-shrub communities. The dominant vascular species on *A. humilis* sites are shadscale and Mormon tea. It was found that *A. humilis* occurred in portions of the habitat where shrubs were relatively less dense. A soil-surface, cryptogamic community contributed 84% or more of the total living cover on sites that supported *A. humilis*. Species composition of the cryptogamic community was highly similar among sites. Likewise, composition of the cryptogamic cover was similar when random samples were compared with samples centered on *A. humilis* plants. The Purgatory Flat site, which does not support the poppy, seems inseparable from *A. humilis* sites in respect to soil characteristics and composition of the associated plant cover. There is reason to believe an *A. humilis* population could be established at the Purgatory Flat site.

Key words: Arctomecon humilis, *dwarf bear-claw poppy, habitat characteristics, gypsophily.*

The dwarf bear-claw poppy (*Arctomecon humilis*) is a perennial herb endemic to gypsum soils of Washington County, Utah (Atwood 1977). It presently occupies an archipelago of isolated sites to the south, west, and east of St. George, all of which are within 8–10 km of the city limits. *A. humilis* is confined to substrates derived from outcrops of certain members of the Moenkopi Formation (USFWS 1985). No detailed discussions of the habitat requirements or general ecology of this species have previously appeared in the literature.

During the last several decades, the development of housing in the St. George–Bloomington area and the construction of Interstate 15 and associated road maintenance facilities have eliminated much of the plant's habitat. Off-road vehicle (ORV) traffic and mineral assessment work on gypsum claims immediately threaten remaining habitat. Off-road vehicles cause excessive erosion and loss of viable *A. humilis* seed stored in the surface soil (Nelson and Harper 1991). Continued development and expansion in the St. George area will undoubtedly result in continued encroachment upon habitat now occupied by the species.

In 1979 the U.S. Fish and Wildlife Service issued a final rule statement declaring *A. humilis* an endangered species (USFWS 1979). Critical habitat was not designated in that ruling. Since 1979, several hundred acres of habitat have been closed to ORV use by the U.S. Bureau of Land Management (USBLM 1987) and the state of Utah, but difficulties in posting and enforcing these closures have resulted in almost no change in patterns of use on habitat occupied by the species. In fact, photographs taken at permanent photo points show an increase in evidence of ORV use on some of these sites over the period 1987–1990. While the direct effects of ORV and mineral exploration on living plants are not always extensive, soil erosion initiated by ORV traffic progressively destroys the limited habitat to which the species is intimately tied. Erosion also results in loss of seed from the soil seed bank. Since the species is short lived (up to perhaps six years), maintenance of viable populations depends upon regular establishment of plants from the seed bank.

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

It is the purpose of this paper to define the habitat requirements of this species.

Study Area

Approximately two-thirds of the habitat occupied by *A. humilis* is on federal land managed by the U.S. Bureau of Land Management (BLM). One-third is owned by the state of Utah and managed by the Utah Department of State Lands and Forestry. The seven poppy sites considered in this paper are managed by the state or by BLM.

In nearly all cases the species is confined to low gypsum hills typically found at the base of red cliffs. The sites are often underlain by similar red beds (see below). The plant occurs occasionally on red gypsum-rich soils but is more typically found on white-gray gypsiferous soils. The white gypsum substrate is almost always associated with a heavy cover of cryptogamic plants (i.e., lichens, mosses, blue-green algae) except where natural erosion and ORV travel have destroyed that cover.

Areas surrounding habitat occupied by the poppy support creosote bush (*Larrea tridentata* [DC.] Cov.) communities. Creosote bush and many of its associates are intolerant of gypsum (Meyer 1986) and are essentially absent from the poppy sites. The gypsum sites support a sparse shrub community that is dominated by burrobush (*Hymenoclea salsola* T. & G.) and shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.). At one site (Beehive Dome) the poppy occurs with the endangered gypsum cactus (*Pediocactus sileri* [Engelm.] L. Benson). Desert tortoises (*Gopherus agassizii* Cooper) have been observed among poppy plants at Red Bluff, but there is no evidence that the tortoises utilize *A. humilis*.

In addition to the seven poppy sites studied, we have sampled another site, Purgatory Flat, which does not support a poppy population. That site is included in the study because it is visually and chemically similar to sites occupied by the species and lies within the range of elevation of those sites. The Purgatory Flat site is only 8 km from existing populations of *A. humilis* at Shinob Kibe Dome near Washington, Utah. The gypsum hills at Purgatory Flat cover a large area extending south from Quail Creek Reservoir for 2.5–3 km. Portions of this area could be used if attempts to establish additional populations of *A. humilis* are ever made.

St. George receives an average of 201 mm of precipitation annually (Brough et al. 1987). Most rainfall occurs during the winter months, but summer (June-September) convective storms contribute about one-fourth of the annual total. Year-to-year variation in total annual precipitation is considerable. The coefficient of variation for total annual precipitation over the past 30 years is 33.2%. A "Walter Diagram" for the St. George weather station (Fig. 1) shows the relationship between annual patterns of precipitation and temperature (Walter 1973). During the winter months, temperatures are low enough and precipitation great enough that soils can accumulate some moisture (striped area in Fig. 1). Warmer temperatures during the spring and summer months create a water deficit, since evaporation exceeds precipitation and moisture is only briefly available to plants (stippled area). Rosettes of *A. humilis* remain green throughout the year and can take advantage of available moisture at any time.

Methods

During 1987 soil was collected at seven *A. humilis* sites: Red Bluff, Price City Hills, White Dome, Shinob Kibe Dome, Boomer Hill, Beehive Dome and Warner Ridge. (The name of the buttelike landform that appears as "Shinob Kibe Dome" on U.S. Geological Survey maps is reported by Gregory [1950] to have been derived from the Piute words *Shinob* [Great Spirit] and *kaib* [mountain]; Gregory considers the name of the geologic member, "Shnabkaib," to be a misspelling of the Piute name.) Soil was also collected at two sites at Purgatory Flat (just below the dike on the southern shore of Quail Creek Reservoir and south of U.S. Highway 17). Soil samples were taken with a 2.5-cm-diameter tube inserted to a depth of 15 cm. A minimum of six samples was collected at each site, the number collected depending upon the size and apparent heterogeneity of the site. Soils at most sites ranged from red, clay-rich to white, purely gypsiferous substrates. Both red and white substrate types were sampled if the poppy occurred on both. Subsamples from each site were combined for analytical purposes, and soils were analyzed by the Brigham

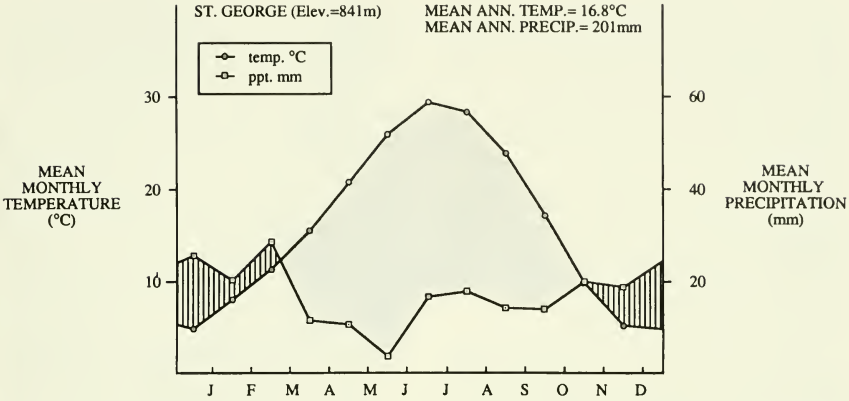


Fig. 1. "Walter Diagram" showing the relationship between average monthly precipitation (mm), along with average monthly temperature (°C) and mean annual temperature and precipitation, for the St. George, Utah, weather station. The stippled area represents a period of water deficit, when evaporation exceeds precipitation and moisture is only briefly available to plants; the striped area is a period when soils may accumulate water.

Young University Soil Laboratory, Department of Agronomy and Horticulture.

Samples were analyzed for concentrations of nine biogenic elements (P, Ca, Mg, K, Na, Zn, Fe, Mn, Cu), pH, electrical conductivity, cation exchange capacity, and linear extensibility (a quantification of a soil's tendency to shrink on drying). Micronutrients (Zn, Cu, Fe, and Mn) were extracted from soils with DPTA (diethylenetriamine-penta-acetic acid). Exchangeable calcium, magnesium, potassium, and sodium were extracted with 1.0 N neutral ammonium acetate. Phosphorus was extracted using 0.5 M sodium-bicarbonate. Individual ion concentrations were determined using a Perkin-Elmer Model 5000 atomic absorption spectrophotometer. Soil reaction was measured with a glass electrode pH meter on saturated soil pastes, and electrical conductivity of the saturated soil paste was measured using a standard wheatstone bridge (U.S. Salinity Laboratory Staff 1954). Cation exchange capacity (CEC) was determined by mass action using a 1.0 normal sodium acetate solution, washing away excess salts with distilled water, and displacing adsorbed sodium with ammonium acetate (Chapman 1965). Linear extensibility was estimated by oven-drying standard diameter cylinders of saturated soil paste for 24 hours and determining percentage change in length.

Results for the preceding suite of soil variables at each of the eight sites were subjected to cluster analysis (Sneath and Sokal 1973) using a program from the Ecology Program Library (W. E. Evenson and J. D. Brotherson, Brigham Young University, Provo, Utah). The values for each parameter at all sites were relativized before being entered in the program (i.e., the largest value for each variable was taken as 100% and all other values were expressed as a percentage of that maximum value). The program computes an index of similarity for all possible site pairs using the formula S. I. = [Σ(minimum values for any attribute for the two sites) /Σ(maximum values for any attribute for the two sites)] × 100 (Ruzicka 1958), where "min" or "max" represents the smallest or largest of the values for each characteristic compared in the two stands.

In 1988 additional soil samples were collected at Beehive Dome, Price City Hills, Red Bluff, and Purgatory Flat. These soil samples were taken as described above. Contents of gypsum, calcium carbonate, sand, skeletal material, and water content at −15 bars matric potential were determined. Percent skeletal material was determined from the weight of the total sample retained on a 2-mm sieve. Percent sand was determined from the weight of material passing a 2-mm sieve (No. 10 mesh) but retained on a 0.05-mm sieve (No. 275 mesh) and is reported as the percentage of the soil fraction less than 2 mm. Alkaline earth carbonates were determined by acid neutralization procedures (U.S. Salinity Laboratory Staff 1954). Gypsum content was determined with a loss-by-weight procedure by drying the soil at 45 C and 105 C, the difference in weight representing the loss of water incorporated into crystals of gypsum (Nelson 1982). Gypsum and calcium carbonate were measured for entire samples, which were ground prior to analysis. Water content was measured across a 15-bar pressure membrane (Richards 1965).

Vegetation was sampled during 1988 at Red Bluff, Price City Hills, and Purgatory Flats. Shrub density and cover, herb cover, and cryptogamic cover were measured along randomly placed 100-m transects. Shrub density was measured using the point-centered quarter method with distance measures taken from points spaced at 10-m intervals along the transect. Two canopy diameter measurements, taken at right angles to each other, were recorded for each shrub included in the sample. Shrub density was computed from the point-to-plant center data (Cottam and Curtis 1956). Shrub cover is based on canopy area of individuals and shrub density data. A nested frequency quadrat frame (Smith et al. 1987) was centered on each of the same points used for the point-quarter sampling and used to evaluate relative frequency and percent cover for cryptogamic species (lichens and mosses), vascular plants, and nonliving cover. At the two poppy sites where vegetation was sampled, Red Bluff and Price City Hills, these procedures were repeated but sampling was centered on the *A. humilis* plant nearest the 10-m point on the transect rather than on the transect line itself. Plant-centered versus random-point locations made it possible to test the hypothesis that the vegetational environment around *A. humilis* plants has a lower shrub density than the general habitat.

RESULTS

Physical Environment

A. humilis was found only on gypsic outcrops of the Moenkopi Formation of Early Triassic age (Fig. 2). The poppy has been reported to be confined to the upper three members: the Upper Red, Shnabkaib, and Middle Red (USFWS 1985). The majority of the populations occur almost exclusively on the Shnabkaib Member (W. Kenneth Hamblin, personal communication). Shnabkaib outcrops also occur in the northwest portion of Purgatory Flat, at the base of red cliffs. The gypsum hills across much of the Purgatory Flat area consist of alluvial sediments derived from the Shnabkaib.

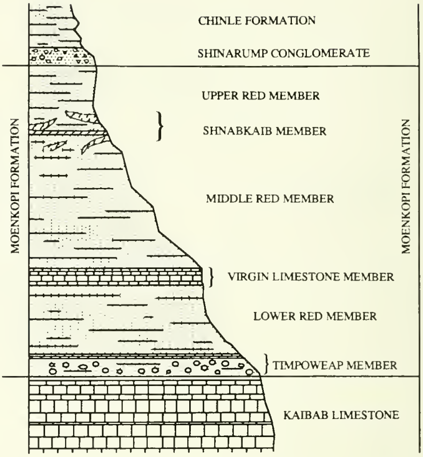


Fig. 2. Diagram showing the relative positions of geologic members of the Moenkopi Formation and adjoining strata in the vicinity of St. George, Utah. (*From:* R. K. Gierisch 1981. Observations and comments on *Pediocactus sileri* in Arizona and Utah. Desert Plants 3: 9–28.)

In Washington County the Shnabkaib Member varies from 80 to 225 m in thickness and consists of white, pink, and light red gypsiferous shale and gypsum (Cook 1960). It is easily recognized by its candy-stripe appearance. In many places surrounding St. George it forms low hills at the bases of red cliffs of the Upper Red Member. These Upper Red cliffs are capped by the Shinarump Conglomerate. A large area of Shnabkaib is bisected by Interstate 15, and an unknown number of acres lie under housing developments in the Bloomington area of St. George and in older sections of St. George itself. The White Hills area west of Bloomington is the largest contiguous portion of exposed Shnabkaib in the vicinity.

Soils on *A. humilis* sites consist of little-altered parent material and are soils only in the broadest definition of the word. There is no obvious horizonation in these substrates, though the uppermost portions would surely be somewhat enriched by additions from the cryptogamic crust and very locally (e.g., at the base of shrubs) by organic amendments from vascular plants. The influence of cryptogams may extend downward into the solum for only a few millimeters. Little organic matter is added to the soil annually, due to sparse vegetative cover. Minimal input of organic matter combined with a dynamic soil surface resulting from dissolution and reformation of gypsum crystals appears to preclude horizon development. The soil survey report for Washington County (USDA 1977) refers to these areas as "badlands" and does not further describe or classify the soils.

Results of soil analyses are shown in Table 1. The heterogeneity of these sites, as discussed above, is reflected in physical and chemical analyses. Within-site variation was considerable (with coefficients of variation exceeding 20%) for all parameters except calcium, electrical conductivity, and pH. In most cases within-site variation for a given variable was as great as that between sites. No site contributed more than one-fourth of the extreme high or extreme low mean values for the various parameters, suggesting that no site, including Purgatory Flat, can be considered chemically distinct from the others. Soils from the Purgatory Flat site show fewer extreme values for the variables considered than do soils from some poppy sites. Furthermore, no raw values for the Purgatory Flat site fall outside the range of values for corresponding variables from poppy sites. The similarity of Purgatory Flat soils to soils at poppy sites is also demonstrated through cluster analysis (Fig. 3), performed as described in Methods.

All soils sampled are slightly basic, with pH in the range of 7.2–7.5, and are highly gypsiferous, with gypsum contents ranging from 27 to 51%. Calcium carbonate content, which ranges from 15 to 24%, is also high. Rasmussen and Brotherson (1986) reported data on soils from desert shrub communities of Washington County that occur adjacent to *A. humilis* habitat. Mean values for pH and CEC presented here for *A. humilis* sites are slightly lower than those reported for the desert shrub soils, but they are within the range of one standard deviation of their mean.

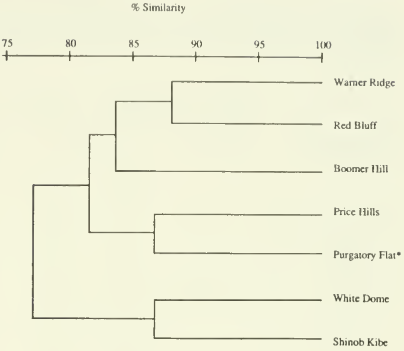


Fig. 3. Dendrogram resulting from clustering of six *A. humilis* sites and one potential *A. humilis* site (Purgatory Flat) for the following soil attributes: P, Ca, Mg, K, Na, Zn, Fe, Mn, Cu, cation exchange capacity, pH, electrical conductivity, and shrinkage upon drying (coefficient of linear extensibility).

Concentrations of magnesium and potassium are 50% lower on the gypsum soils, while levels of phosphorus and zinc are not different. The most striking differences are between concentrations of calcium, copper, and iron. Levels of calcium and copper are 10 times greater in *A. humilis* soils, while iron concentrations are the same magnitude lower. Obviously, these disparities have not interfered with the growth of *A. humilis*, and there is little evidence to suggest that such abnormal values are required for its existence. Meyer (1986) concludes that the likelihood of chemical factors controlling species composition on gypsum soils is minimal, and that the degree of endemism on gypsum soil is due to physical properties of the soil that affect available moisture for plant growth.

Soil texture is not reported here because of difficulties in textural determination created by properties of these soils: high concentrations of salt cause fine particles to become flocculated, thus rendering hydrometric procedures useless, and gypsum crystals complicate particle size determination through sieving. It is likely that much of the sand-size component, as measured here by sieving, consists of gypsum. The percentage of sand-size particles in the soil fraction smaller than 2 mm ranges from 14 to 29%, leaving three-fourths of the weight of the <2 mm material to

TABLE 1. Mean values for selected chemical and physical soil parameters at seven *A. humilis* sites and one potential *A. humilis* site (Purgatory Flat). Standard error is shown in parentheses. Elemental analyses were not run for the Beehive Dome site. Values are not available for the last five parameters at Boomer Hill, Shinob Kibe, Warner Ridge, and White Dome.

	Beehive Dome	Boomer Hill	Price Hills	Red Bluff	Shinob Kibe	Warner Ridge	White Dome	Purgatory Flat
Nutrients (ppm)								
P	—	17.0 (5.89)	33.7 (1.43)	22.9 (2.76)	19.4 (8.14)	5.9 (0.62)	8.8 (1.71)	33.8 (5.34)
Ca (ppm × 10^{-4})	—	3.6 (0.19)	3.7 (0.22)	4.0 (0.13)	4.2 (0.11)	4.0 (0.10)	3.9 (0.09)	4.1 (0.07)
Mg	—	97.6 (7.74)	76.3 (3.82)	73.9 (4.87)	60.8 (6.79)	81.2 (6.25)	57.6 (8.12)	74.3 (5.14)
K	—	105.9 (9.24)	82.6 (4.63)	74.1 (4.71)	46.3 (9.07)	78.6 (6.79)	42.9 (10.1)	74.6 (11.53)
Na	—	15.2 (1.39)	15.3 (0.63)	13.7 (0.70)	14.2 (1.37)	14.2 (0.57)	11.6 (0.43)	14.4 (0.85)
Zn	—	0.4 (0.02)	0.4 (0.03)	0.3 (0.02)	0.2 (0.02)	0.3 (0.03)	0.3 (0.04)	0.5 (0.22)
Fe	—	2.9 (0.12)	2.6 (0.25)	2.5 (0.15)	1.8 (0.06)	2.9 (0.19)	1.9 (0.11)	2.1 (0.19)
Mn	—	1.5 (0.08)	1.2 (0.03)	1.3 (0.08)	1.0 (0.15)	1.1 (0.16)	1.0 (0.10)	1.1 (0.17)
Cu	—	0.9 (0.07)	0.9 (0.04)	0.8 (0.10)	1.0 (0.35)	0.9 (0.10)	0.9 (0.10)	1.6 (0.73)
CEC[1]	—	9.6 (0.50)	7.4 (0.23)	8.2 (0.40)	6.0 (0.49)	7.7 (0.50)	5.5 (0.61)	7.4 (0.50)
pH	—	7.3 (0.07)	7.3 (0.06)	7.2 (0.05)	7.3 (0.10)	7.5 (0.03)	7.3 (0.06)	7.4 (0.05)
EC[2]	—	2.2 (0.06)	2.2 (0.10)	2.4 (0.05)	2.2 (0.05)	2.2 (0.03)	2.2 (0.06)	2.2 (0.05)
COLE[3]	—	1.3 (0.21)	0.8 (0.17)	1.0 (0.19)	0.7 (0.48)	1.0 (0.19)	0.4 (0.18)	0.9 (0.20)
%H_2O −15 bar	11.4 (0.81)	—	8.2 (2.26)	11.8 (2.42)	—	—	—	14.6 (1.18)
$CaCO_3$ (% by wt.)	15.4 (0.52)	—	24.3 (0.09)	22.6 (1.85)	—	—	—	18.8 (2.31)
$CaSO_4$ (% by wt.)	32.7 (4.70)	—	27.3 (12.22)	39.3 (15.38)	—	—	—	51.1 (5.36)
Sand (% of <2mm)	14.6 (2.71)	—	26.0 (5.19)	24.2 (8.99)	—	—	—	29.0 (4.39)
Skeletal (% of total)	14.3 (2.55)	—	18.1 (9.02)	16.9 (10.27)	—	—	—	9.0 (3.08)

[1] CEC = cation exchange capacity in meq per 100 g of soil.
[2] EC = electrical conductivity in mmho/cm.
[3] COLE = coefficient of linear extensibility: 0 = shrinkage, 1 = <3% shrinkage, 2 = 3–6% shrinkage.

be contributed by silt- and clay-size particles. The large proportion of fine particles is congruous with the prevalence of shales in the Shnabkaib and adjacent geologic members. Shrinkage of saturated soil pastes upon drying (coefficient of linear extensibility) ranged from 0 to 6%, the higher values suggesting that the finer materials in some of the soils include expanding clays.

Biotic Associates

Total living cover on the three sites sampled ranged from 37 to 59% (Table 2). Differences between values measured for that variable at random points and at *A. humilis*–centered points are small and probably not significant. (Total cover values could not be tested for significance because data for shrubs were collected by a method different

TABLE 2. Percent absolute living cover and percent relative cover contributed by groups of nonvascular and vascular plants for general habitats and for habitats at *A. humilis*–centered sampling points at two *A. humilis* sites (Price City Hills and Red Bluff) and for the general habitat at one gypsiferous site on which an *A. humilis* population does not now exist (Purgatory Flat). Trace amounts are noted "T".

	Price City Hills		Red Bluff		Purgatory Flat
	Random points	*A. humilis* centered	Random points	*A. humilis* centered	(Potential *A. humilis* site)
Absolute living cover (%)	46.7	46.2	37.2	31.2	59.6
Relative cover (%)					
Nonvascular (total)	(93.7)	(96.0)	(84.0)	(92.1)	(88.1)
Lichens					
Collema tenax	70.9	64.9	61.6	58.0	65.6
Psora dicipiens	17.4	28.4	19.0	32.0	15.7
Other	5.4	2.7	1.1	2.0	6.8
Moss	T	T	2.2	T	1.2
Vascular (total)	(6.3)	(4.0)	(16.0)	(7.9)	(11.9)
Grasses and forbs		1.6	1.1		1.9
Shrubs					
Atriplex confertifolia	1.6	0.4	4.3	1.9	3.2
Ephedra torreyana	2.2	1.4	4.5	4.2	3.5
Hymenoclea salsola	1.4	0.2	5.0	0.9	1.5
Other	1.1	0.6	1.0	1.2	1.8

from that used for nonvascular plants and forbs.)

Nonvascular plants contributed 84% or more of the total living cover at all sites (Table 2). Lichens were the most important component of the nonvascular plant cover and total living cover measured. Species composition and cover at the three sites and at both random and poppy-centered points were similar. The lichens, *Collema tenax* (Sw.) Ach. and *Psora decipiens* (Hedw.) Hoffm., were the most common species at all sites, the former accounting for 58–71% of the lichen cover, and the latter 16–32%. Grasses and forbs contribute little to the total cover on these sites and in two cases were not encountered in sampling (Table 2). Many species of grasses and forbs on these sites are annuals and are present only during a part of the year. Red brome (*Bromus rubens* L.), an introduced species, is the most common annual on these sites, through it was not frequently encountered in quadrats. It grows in abundance only at the base of shrubs and is rarely associated with *A. humilis* plants.

Shrub densities measured at random points and at *A. humilis*–centered points at Price City Hills and Red Bluff, and at random points at Purgatory Flat, are reported in Table 3. Differences among shrub densities were tested for significance using a least significant difference method at the alpha = .05 level (Steele and Torrie 1960). Analysis was based on point-to-plant distances. Shrub density at the Purgatory Flat site was not different from that measured at random points at Red Bluff and *A. humilis*–centered points at Price City Hills. Densities measured from random points and from *A. humilis*–centered points differed significantly at the latter two sites, though the density at random points at Price City Hills was not significantly different from the density at *A. humilis* points at Red Bluff. It thus appears that within each habitat, the poppy occupies portions of the habitat where shrubs are relatively less dense.

Shrub species composition was similar at all three sites with the exception of the presence of bursage (*Ambrosia dumosa* [Gray] Payne) at Purgatory Flat. This species contributed 15% of shrub individuals at that site. At Price City Hills, *Lepidium fremontii* Wats., a suffrutescent subshrub, had a relative density of 60%, but only 5–6% at other sites. While *Lepidium* was common on the Price City Hills site, individual plants were small (mean area of 73 cm^2) and contributed less than 5% of the total living cover. All three sites are dominated by shadscale and Mormon tea (*Ephedra torreyana* Wats.), while adjacent areas are dominated by creosote bush and blackbrush (*Coleogyne ramosissima* Torr.) (Rasmussen and Brotherson 1986).

TABLE 3. Total shrub density for the general habitat and for *A. humilis*–centered sampling determined with the point-quarter method at two *A. humilis* sites (Price City Hills and Red Bluff) and for the general habitat at one non-*A. humilis* site (Purgatory Flat). Relative density for major shrub species is based on the sample taken with the quarter method. Shrub density differences among sites were tested for statistical significance: means followed by the same letter in subscript do not differ significantly.

	Price City Hills		Red Bluff		Purgatory Flat
	Random points	*A. humilis* centered	Random points	*A. humilis* centered	(Potential *A. humilis* site)
Total shrub density (no./ha)	2365_c	1286_b	1515_b	636_a	1759_b
Relative density (%)					
Ambrosia dumosa					15.0
Atriplex confertifolia	25.0	18.9	47.5	48.8	45.6
Ephedra torreyana	8.8	8.8	15.8	30.0	11.3
Hymenoclea salsola	5.0	3.8	28.3	11.3	18.1
Larrea tridentata					0.6
Lepidium fremontii	60.0	66.3	6.7	5.0	5.0
Lycium andersonii	1.3	2.5		5.0	0.6
Psorothamnus fremontii			1.7		2.5
Stanleya pinnata					1.3

DISCUSSION

A. humilis sites studied are similar with regard to physical and biological parameters. All occur on the same geologic member within an elevational range of 750–1050 m. Each site is heterogeneous with regard to the soil parameters measured, but no site appears to be exceptionally different from all others as might be predicted, since all sites are on a common parent material. Species composition of the vascular and nonvascular plant communities studied was similar for all sites. All gypsiferous sites were dominated by shadscale and Mormon tea. Creosote bush dominated areas immediately adjacent. Within its habitat *A. humilis* was found to occupy areas that have a lower shrub density relative to the general habitat. No difference in cryptogamic plant cover could be detected for areas surrounding *A. humilis* plants relative to the general habitat.

The Purgatory Flat site does not appear to differ significantly from *A. humilis* habitats for any of the parameters studied. It seems likely that *A. humilis* could survive and reproduce on in-place outcrops of the Shnabkaib at this site. Distance from St. George makes this site less likely to be threatened by development; and intensity of ORV traffic, as evidenced by tracks and trails, is considerably less than on most *A. humilis* sites. The outcrops of Shnabkaib along the north end of the basin lie in a narrow strip between state highways 9 and 17 and cliffs formed by the Upper Red, making it possible to protect the site by fencing along two sides only. For purposes of habitat protection, portions of the Purgatory Flat area should receive status similar to *A. humilis* sites.

A. humilis is strictly associated with a unique and limited habitat, and maintenance of viable populations of the species requires the protection of this habitat, much of which is impacted by cultural disturbances. All of the sites studied show damage to the habitat, particularly to the cryptogamic plant cover, and to *A. humilis* plants directly. Most damage is related to ORV use. Recent surface mineral assessment work at two sites has resulted in the disturbance of soil surfaces and the destruction of plants. The rapid growth of St. George and associated new developments poses inevitable threats. Although critical habitat was not defined for the species in the 1979 mandate that gave it protection under the Endangered Species Act, continuing habitat degradation over the last 10 years suggests that such designation is appropriate. If this species is to be preserved, portions of the habitat must be protected from development and ORV traffic. Establishment of additional populations on unoccupied outcrops of suitable habitat should be attempted while genetic diversity is still available.

ACKNOWLEDGMENTS

This study was funded in part by a grant from the Utah Native Plant Society. Financial assistance was also provided by the U.S. Bureau of Land Management. Figure 2 was provided by Ralph Gierisch (Rare Plants Consultant, St. George, Utah) and reprinted with his permission. W. Kenneth Hamblin (Geology Department, Brigham Young University) interpreted the geologic associations at the various *A. humilis* sites.

LITERATURE CITED

ATWOOD, N. D. 1977. The dwarf bear-poppy. Mentzelia 3: 6–7.

BROUGH, R. C., D. L. JONES, AND D. J. STEVENS. 1987. Utah's comprehensive weather almanac. Publisher's Press, Salt Lake City. 517 pp.

CHAPMAN, H. D. 1965. Cation exchange capacity. Pages 899–900 *in* C. A. Black, ed., Methods of soil analysis, part 2. American Society of Agronomy, Madison, Wisconsin.

COOK, E. F. 1960. Geologic atlas of Utah: Washington County. Bulletin 70, Utah Geological and Mineralogical Survey.

COTTAM, G., AND J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. Ecology 37: 451–460.

GREGORY, H. E. 1950. Geology and geography of the Zion Park region, Utah and Arizona. Geological Survey Professional Paper 220.

MEYER, S. E. 1986. The ecology of gypsophile endemism in the eastern Mojave Desert. Ecology 67: 1303–1313.

NELSON, D. R., AND K. T. HARPER. 1991. Demographic and seed bank biology of *Arctomecon humilis* (Papaveraceae), a short-lived perennial herb. In preparation.

NELSON, R. E. 1982. Carbonate and gypsum. Pages 181–197 *in* C. A. Black, ed., Methods of soil analysis, part 2. 2d ed. American Society of Agronomy, Madison, Wisconsin.

RASMUSSEN, L. L., AND J. D. BROTHERSON. 1986. Habitat relationships of sandsage (*Artemisia filifolia*) in southern Utah. Pages 58–66 *in* E. D. McArthur, and B. L. Welch, compilers, Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*. USDA Forest Service General Technical Report INT-200.

RICHARDS, L. A. 1965. Physical condition of water in soil. Pages 134–135 *in* C. A. Black, ed., Methods of soil analysis, part 1. American Society of Agronomy, Madison, Wisconsin.

RUZICKA, M. 1958. Anwendung Mathematisch-Statishticher Methoden in Der Geobotanik (Synthetische Bearbeitung von Aufnahme). Biologia, Bratisl. 13: 647–661.

SMITH, S. D., S. C. BUNTING, AND M. HIRONAKA. 1987. Evaluation of the improvement in sensitivity of nested frequency plots to vegetational change by summation. Great Basin Naturalist 47: 299–307.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco. 573 pp.

U.S. BUREAU OF LAND MANAGEMENT. 1987. Off-road vehicle closure, Utah. Federal Register 52(49): 7941.

USDA SOIL CONSERVATION SERVICE AND USDI BUREAU OF LAND MANAGEMENT AND NATIONAL PARK SERVICE. 1977. Soil survey of Washington County area, Utah. Washington, D.C. 140 pp.

U.S. FISH AND WILDLIFE SERVICE. 1979. Determination that *Arctomecon humilis* is an endangered species. Federal Register 44(216): 64250–64252.

——. 1985. Dwarf bear-poppy recovery plan. USFWS Region 6, Denver, Colorado. iv + 26 pp.

U.S. SALINITY LABORATORY STAFF. 1954. Diagnosis and improvement of saline and alkali soils. Agricultural Handbook No. 60. USDA, Washington, D.C. 157 pp.

WALTER, H. 1973. Vegetation of the earth. Springer-Verlag, New York. 237 pp.

Received 15 November 1990
Revised 6 March 1991
Accepted 28 March 1991

Great Basin Naturalist 51(2), 1991, pp. 176–182

BROMUS INVASIONS ON THE NEVADA TEST SITE: PRESENT STATUS OF *B. RUBENS* AND *B. TECTORUM* WITH NOTES ON THEIR RELATIONSHIP TO DISTURBANCE AND ALTITUDE

Richard Hunter[1]

ABSTRACT.—*Bromus rubens* and *Bromus tectorum* are now nearly ubiquitous components of the Nevada Test Site (NTS) flora. Introduced to the western United States in the late 1800s, they spread through the Mojave and Great Basin deserts in the early twentieth century. Since quantitative studies began on the NTS in 1957, *Bromus* spp. have greatly increased in frequency and density. By 1988 both species occurred in many places at densities exceeding 1000 individuals per square meter. They may significantly increase flammability of the vegetation and reduce success of native ephemeral species.

Key words: Bromus rubens, Bromus tectorum, *Nevada Test Site, introduced species, fire propagation, fire recovery.*

In the roughly 150 years of American settlement of the western United States approximately 20 species of *Bromus* have been introduced (Munz 1968). Of these species, two, *Bromus tectorum* and *B. rubens*, have dramatically spread over rangelands. In the Great Basin Desert *B. tectorum* has had major impacts on rangelands and agricultural yields (e.g., Morrow 1984), and in parts of California and the Mojave Desert *B. rubens* has come to dominate the annual plant floras.

The Nevada Test Site (NTS) is a 1350-square-mile enclave straddling the boundaries and transition zone between the Mojave and Great Basin deserts (Fig. 1). Eight *Bromus* species occur on the NTS, six of them introduced (Beatley 1976). Both *B. rubens* and *B. tectorum* are now widespread and significantly affect the NTS ecology. This paper is an attempt to document the present status of these two species and provide information on the nature of their increase in abundance.

History of *Bromus* Introductions

Bromus rubens

Frenkel (1970) considered *B. rubens* to have been introduced during the Mexican occupation of California between 1825 and 1848, and S. B. Parish called an 1889 roadside specimen from San Bernardino County, California, "a recent introduction" (California Academy of Science Herbarium). In the Mojave Desert it was not seen on an 1891 expedition to Death Valley (Coville 1893). M. E. Jones first collected *B. rubens* in 1907 at Searchlight, Nevada (Rancho Santa Ana Herbarium). Mrs. F. P. Morris collected it at Mojave, California, in 1917 (California Academy of Science Herbarium). V. Duran, in 1933, called it a "common grass between Mojave and Palmdale along roadsides and on cleared land" (Intermountain Herbarium, Utah State University). On the eastern edge of the Mojave, E. Snow collected *B. rubens* in 1931 near St. George, Utah (University of California, Davis Herbarium, Crampton Collection).

Near the NTS, I. W. Clokey (1951) collected plants in the Charleston Mountains from 1937 through 1941. He collected *B. rubens* from only one location, at 1550 m (5085 ft) in a disturbed area of the "juniper belt." The distribution on that specimen label was noted as "roadsides and waste places." O. V. Deming collected specimens of *B. rubens* on the Desert National Wildlife Range (directly east of the NTS) in 1946 (University of Nevada, Las Vegas Herbarium).

It appears, therefore, that *B. rubens* invaded the Mojave Desert during the 1920s, spreading first to disturbed areas. It was not common, however, until after 1950. By 1963

---

[1] U.S. Department of Energy Basic Environmental Compliance and Monitoring Program (BECAMP), Reynolds Electrical & Engineering Co., Inc., Environmental Health Division, Applied Studies Group, Box 98521, Las Vegas, Nevada 89193–8521.

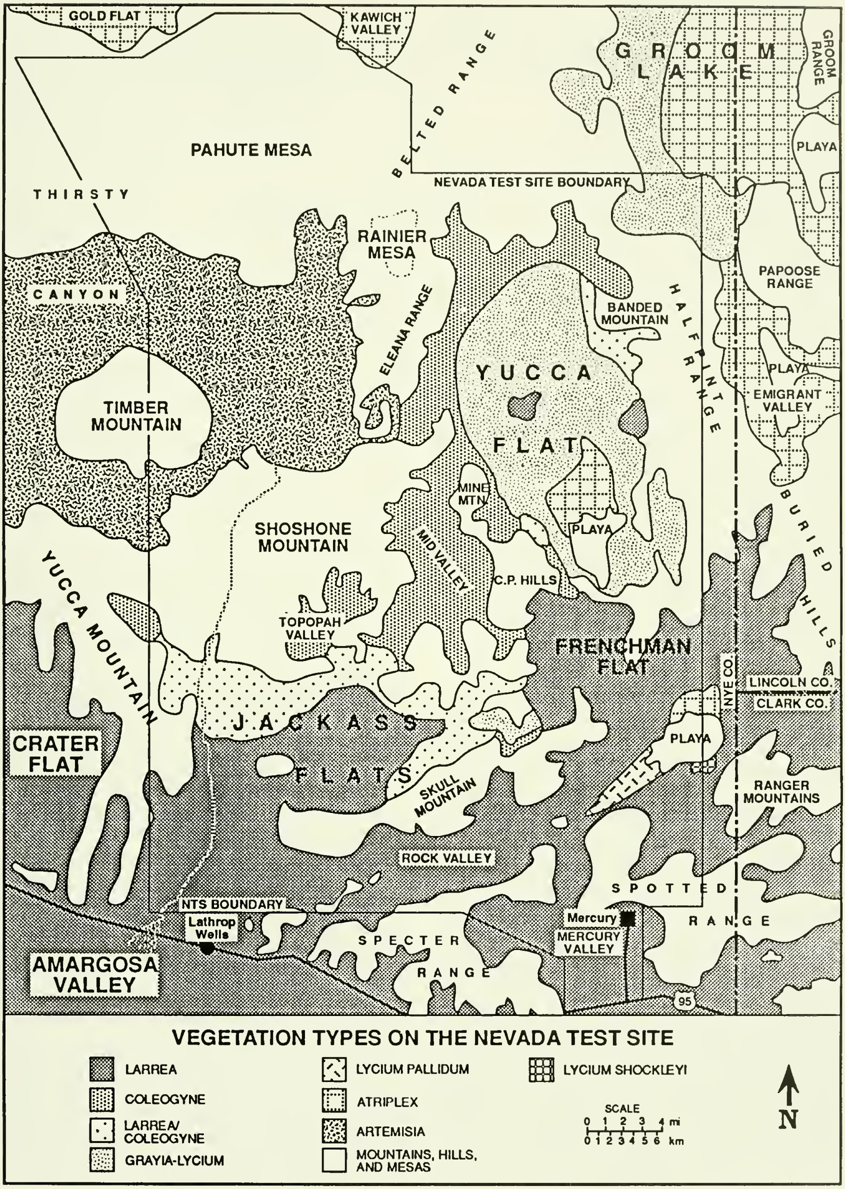

GOLD FLAT
KAWICH VALLEY
BELTED RANGE
GROOM LAKE
GROOM RANGE
PAHUTE MESA
PLAYA
NEVADA TEST SITE BOUNDARY
THIRSTY
CANYON
RAINIER MESA
ELEANA RANGE
PAPOOSE RANGE
BANDED MOUNTAIN
HALFPINT RANGE
YUCCA FLAT
TIMBER MOUNTAIN
EMIGRANT VALLEY
MINE MTN
PLAYA
BURIED HILLS
SHOSHONE MOUNTAIN
MID VALLEY
C.P. HILLS
YUCCA MOUNTAIN
TOPOPAH VALLEY
FRENCHMAN FLAT
NYE CO.
LINCOLN CO.
CLARK CO.
CRATER FLAT
JACKASS FLATS
PLAYA
SKULL MOUNTAIN
RANGER MOUNTAINS
ROCK VALLEY
SPOTTED RANGE
NTS BOUNDARY
Lathrop Wells
Mercury
MERCURY VALLEY
SPECTER RANGE
AMARGOSA VALLEY
95
VEGETATION TYPES ON THE NEVADA TEST SITE
LARREA
COLEOGYNE
LARREA/COLEOGYNE
GRAYIA-LYCIUM
LYCIUM PALLIDUM
ATRIPLEX
ARTEMISIA
MOUNTAINS, HILLS, AND MESAS
LYCIUM SHOCKLEYI
SCALE
0 1 2 3 4 mi
0 1 2 3 4 5 6 km
N

Fig. 1. Major landforms and vegetative communities on the NTS as determined by Beatley (O'Farrell 1976).

it was abundant on the NTS at elevations of 1219–1524 meters (4000–5000 feet), though infrequent in the *Larrea tridentata* associations below that altitude (Beatley 1966).

Bromus tectorum

The spread of *B. tectorum* has been described by several other authors and occurred primarily at higher altitudes and latitudes than that of *B. rubens*. It was first recognized in 1861 (Morrow and Stahlman 1984, citing Hitchcock 1950). Mack (1981) described the invasion of *B. tectorum* into western North America, a process that he considered completed by roughly 1928. Yensen (1981) and Morrow and Stahlman (1984) also reviewed this process.

Mojave Desert collections of *Bromus tectorum* were rare before 1950. Clokey (1951) cited six collections of *B. tectorum* in the Charleston Mountains during the late 1930s. F. W. Gould collected it in 1942 as a roadside weed in St. George, Utah, and P. Dalley (1943) and O. V. Deming (1946) collected *B. tectorum* on the Desert National Wildlife Range (University of Nevada, Las Vegas herbarium). Beatley (1966) reported it on the NTS in disturbed patches above 1524 m (5000 ft).

METHODS

Plots for studies since 1987 were selected to be representative of either a particular disturbance or an undisturbed area nearby. Some plots were considered pristine, chosen specifically for lack of disturbance. *Bromus* densities were not considered when selecting a site. Altitudes of sampled locations were determined from United States Geological Survey 7.5-minute topographical maps.

Twenty .025-m^2 randomly placed quadrats within 1000-m^2 plots were used to monitor ephemeral plants (1987–1990). Monitoring also included harvesting of all annual plants within each quadrat. New quadrat locations were selected within approximately the same 1000 m^2 every year. Harvested plants were oven-dried at 66 C for three days, then equilibrated with room air before weighing.

RESULTS

Present Distribution

The distributions of the two *Bromus* species with respect to altitude and disturbance are shown in Table 1. *B. rubens* was present at all but one sampled location (Rainier Mesa, 2286 m [7500 ft]). It was present at less than two plants per square meter at only two locations, Jackass Flats and Pahute Mesa. The former was an area of deep, sandy soil at 945 m (3100 ft), near the lowest altitude on the NTS, and the latter was in an established *Artemisia nova* community at 1890 m (6200 ft), above the normal distribution zone for *B. rubens*. It was therefore essentially ubiquitous on the NTS below 1524 m (5000 ft). At four locations sampled in both 1987 and 1988, population densities increased an average of threefold (3.38 ± 0.89, sem), indicating both good reproduction in 1987 and good germination in 1988 (Table 1). The median density in 1988 was 362 ± 84 plants per square meter (± sem; 19 sites). The highest densities were found on areas where soils were softened and shrubs killed by gopher and small mammal activities, but several undisturbed locations had densities over 1000/m^2.

The populations of *B. rubens* were heavily infested with a smut (*Ustilago bullata* Berkeley) fungus. In 1987 the smut was present on 0–36% of *Bromus rubens* plants on 5 sites; in 1988 it ranged from 0% to 43% on 17 sites, with an average (± sem) of 15 ± 3%. The smutted plants produced no viable seed. Presumably this disease significantly reduced seed production. However, smut was noted by others in early populations (e.g., A. A. Beetle 1941, University of California, Berkeley Herbarium), and it apparently did not prevent increases in density.

In the early 1980s *Bromus tectorum* became noticeably common below 1524 m (5000 ft). In Yucca Flat on some of the ground zeroes (GZs are areas denuded by nuclear bomb blasts in the 1950s and early 1960s) it was seen in apparent near-monoculture patches surrounded by *B. rubens* monocultures. In Mercury townsite (the NTS base camp) it occurred in the vicinity of buildings and roads associated with *B. rubens*, while away from disturbance it was absent. In 1983 in the blast zone surrounding Sedan Crater, which resulted from a peaceful nuclear explosion excavation experiment, *B. rubens* was seen at all 12 sites on which perennials were measured, and *B. tectorum* was also present at 6 of those sites (Hunter and Romney, unpublished observations).

TABLE 1. Densities of *Bromus rubens* and *B. tectorum* (n/m^2 ± sem) in 1987 (*) and 1988 in relation to disturbance and altitude (m).

Location	Disturbance	Altitude	*B. rubens*	*B. tectorum*
Jackass Flats	none	950	+*	0
Jackass Flats	none	950	16 ± 14	+
Frenchman Flat	gopher	960	2644 ± 716*	+*
Frenchman Flat	none	975	48 ± 35*	0*
			258 ± 153	4 ± 4
Frenchman Flat	none	1000	34 ± 22	0
Frenchman Flat	roadside	1000	4 ± 3	0
West Mercury Valley	gopher	1040	3550 ± 366	0
Rock Valley	none	1070	754 ± 298*	0*
			2034 ± 632	+
Mercury town	none	1150	352 ± 120*	+*
			446 ± 130	2 ± 2
Mercury town	shrubs removed	1150	456 ± 192*	+*
			1912 ± 476	8 ± 7
East Yucca Flat	none	1240	652 ± 328	+
Southwest Yucca Flat	none	1250	1872 ± 556	20 ± 11
West Yucca Flat	none	1280	188 ± 49	2 ± 2
West Yucca Flat	ground zero	1290	1472 ± 356	1884 ± 396
Southwest Yucca Flat	none	1300	1803 ± 474*	0
Southwest Yucca Flat	fire—1985	1300	720 ± 168*	+*
North Yucca Flat	Sedan GZ	1325	19 ± 11	1155 ± 431
North Yucca Flat	Sedan GZ	1325	324 ± 154	2004 ± 424
North Yucca Flat	none	1325	142 ± 69	2 ± 2
Northwest Yucca Flat	none	1400	658 ± 344	4 ± 4
Northwest Yucca Flat	T2 GZ	1400	774 ± 169	+
South Mid-valley	none	1463	362 ± 84	414 ± 152
South Mid-valley	fire—1986	1463	114 ± 37	3916 ± 752
Pahute Mesa	none	1900	+	+
Rainier Mesa	none	2300	0	0

Bromus tectorum densities in 1987–88 differed considerably from those of *B. rubens*. This species was absent or at densities $< 2/m^2$ below 1219 m (4000 ft). Above that altitude it was present at $>1000/m^2$ on several burned and GZ areas. It was not dense on all disturbed sites above 1219 m, however, as seen on the 1985 fire area and T2 GZ (Table 1). Its distribution was therefore considerably patchier than that of *B. rubens*, and it was associated more strongly with disturbance.

Data on plant size from locations where the two species occurred together show that *Bromus tectorum* is the larger of the two species ($p < .02$; Wilcoxon Signed Rank Test: Ostle 1963) and may therefore have a competitive advantage (Table 2). The vegetative and seed characteristics of the two species are very similar, and I would expect seed production to be similarly proportional to plant weight in both.

TABLE 2. Average weights per plant (mg ± sem) of *B. rubens* and *B. tectorum* when growing at the same location.

Site	*Bromus rubens*	*Bromus tectorum*
Disturbed		
Mid-valley	26 ± 11	33 ± 7
Yucca Flat–Sedan	23 ± 9	47 ± 13
Yucca Flat–Sedan	9 ± 2	19 ± 6
Yucca Flat–T1 GZ	11 ± 3	17 ± 4
Pristine		
Mid-valley	11 ± 1	20 ± 2
Yucca Flat–001a	14 ± 2	23 ± 6
Yucca Flat–001b	16 ± 2	38 ± 2

DISCUSSION

A comparison of these recent data with those taken earlier demonstrates a significant increase in both frequencies and densities over the past 30 years. The earliest data taken in association with the nuclear bomb testing program were from 1957 to 1959 (Shields and Rickard, unpublished reports). They reported cover data, which could not be directly compared to our density data. However, in three valleys (Yucca Flat, Frenchman Flat, and Jackass Flats; altitudes 945–1524 m) Shields and Rickard measured ephemeral plants at 41 plots and found *Bromus rubens* at only 22 of them (54%). In 1987–88 I found *B. rubens* in those same three valleys at all 21 plots sampled (significantly different by chi square at $p < .001$). Similarly, Beatley (1966) reported *B. rubens* at 8 of 18 plots in Yucca Flat in 1964, while I found it at all 11 sampled locations (significant at $p < .01$). At the two sites where a direct comparison was reasonable, Beatley found 0.0, and 0.2 *B. rubens* per square meter in 1964, while I found 1803 ± 474 and 1434 ± 304 per square meter in 1987–88. At an undisturbed site near the Sedan GZ Martin (unpublished) found 0.6 *B. rubens* per square meter, while in 1988 at the same location I found 142 ± 69.

The most complete time series is for a small area in Rock Valley where records of Beatley, U.S. Desert Biome/International Biological Program researchers, and our studies are available covering 20 of the 26 years since 1962. Table 3 shows that there was an increase from fewer than 10 *B. rubens* per square meter in the 1960s and early 1970s to thousands per square meter in the late 1980s. This increase began in 1974, following the excellent growth year of 1973. Since then, years of good growth have resulted in a stairstep amplification of *B. rubens* population density. At the same time the populations of native annuals fluctuated without any dramatic trends toward increased or decreased density (Table 3). In 1989 and 1990 drought prevented germination of ephemeral plant species.

Biomass data from U.S. International Biological Program Desert Biome studies and our results show trends similar to those on density (Table 4). That is, *B. rubens* greatly increased in biomass at the same time it increased in density, while biomass of native species was highly variable without demonstrating any trends. Proportionately, *Bromus* biomass increased from approximately 10% of ephemeral biomass to 97% between 1972 and 1988.

Differences in sampling techniques and areas sampled, coupled with a naturally high year-to-year variability in richness, prevented any significant diversity comparisons among data of Shields, Beatley, IBP/Desert Biome, and BECAMP studies. However, high *B. rubens* densities resulting from irrigation and fertilization treatments were associated with a decrease in species richness of native species (Hunter, in press).

TABLE 3. Densities of *Bromus rubens* (n/m^2) and native species measured in several adjacent Rock Valley plots between 1963 and 1974.

Year	*Bromus rubens*	Natives
1963[1]	5.0	10.0
1964[1]	6.2	27.6
1965[1]	2.2	2.4
1966[1]	3.2	69.6
1967[1]	3.6	7.0
1968[1]	7.6	99.6
1969[1]	14.0	109.8
1970[1]	19.8	14.0
1971[1]	0.2	2.0
1972[1]	0.0	3.0
1973[3]	0.4	118
1974[2]	11.2	101
1975[2]	13.2	216
1976[2]	90.9	327
—	—	—
1983[4]	89	108
1984[4]	167	19
1985[4]	156	111
1986	—	—
1987[5]	754 ± 298	100 ± 22
1988[5]	2034 ± 632	86 ± 33
1989[5]	0 ± 0	0 ± 0
1990[5]	16 ± 16	0 ± 0

[1] Beatley, unpublished
[2] Turner 1972–1976
[3] Turner and McBrayer 1974
[4] R. B. Hunter and K. B. Hunter, unpublished
[5] This paper

TABLE 4. Biomasses (g/m^2) of *Bromus rubens* and native species in Rock Valley. Data for the 1970s are from Turner 1972–76, Turner and McBrayer 1974, and Turner, unpublished.

Year	*Bromus rubens*	Natives
1971[1]	0.10	0.54
1972[1]	0.04	0.40
1973[2]	1.29	78.9
1974[1]	0.83	1.50
1975[1]	2.13	22.5
1976[3]	3.25	12.0
—	—	—
1987	17.0	0.51
1988	34.0	0.9
1989	0.0	0.0
1990	0.0	0.0

Bromus tectorum

Beatley (1966) described the status of *B. tectorum* as present only above 1524 m (5000 ft), largely in disturbed areas of *Artemisia tridentata*–dominated vegetation. This constrasts with my data (Table 1), which demonstrated a significant presence of *B. tectorum* throughout Yucca Flat, 1219–1524 m (4000–5000 ft) in the late 1980s.

The propensity of the *Bromus* species to carry fire has been frequently noted (e.g., Stewart and Hull 1949, Beatley 1966, Yensen 1981). The dead stems and litter persist for a year or two and serve to carry fire across bare areas between shrubs and trees. On the NTS this is true for both *B. rubens* and *B. tectorum*. On the NTS fires burned an estimated 38,000 acres between 1978 and 1987 (R. R. Gudeman, personal communication), in spite of active control efforts. The *Bromus* species were significantly present both in control and previously burned areas (Table 1), suggesting a role both in fire propagation and recovery of vegetation following fire.

The effects of the *Bromus* populations on native ephemerals were not clear. Table 4 shows no significant downward trend in native population densities. The native ephemerals behaved somewhat differently from *B. rubens*, however. Following two very dry years (1971, 1972), the native species rebounded immediately (1973 was an unusually wet spring), while the *B. rubens* population required two years to reach its previous density. The native seeds therefore seemed better adapted than the *B. rubens* seeds to weather the severest drought, while the *Bromus* species appeared to reproduce better in the "normal" years. The driest and least productive years of record were 1989 and 1990, but the consequences are as yet unknown.

Some adaptations that give *Bromus* species advantages over desert ephemerals include better seed dispersal adaptations than natives (see Ellner and Shmida 1981, Levin et al. 1984), a greater response to nitrogen by the introduced grasses (Hunter, unpublished data), and a greater proportion of *Bromus* plants inhabiting the fertile soils under shrubs (Soholt and Irwin 1976, R. B. Hunter and K. B. Hunter, unpublished data). One disadvantage that seemed to limit *Bromus* growth in certain years was the fibrous root systems of the grasses as opposed to tap roots of the natives—sparse, frequent rains favored *Bromus*, while deep, infrequent ones favored species with tap roots. Given these genetic differences, one might expect the introduced grasses to find slightly different niches from the natives and possibly add to the diversity of the native flora, rather than diminish it. In the densities occurring in recent years, however, the environment of the desert surface appears to this author to be radically changed. I suspect that the surface shading by dead *Bromus* stalks, the changed fire frequencies, and the dense population of the introduced *Bromus* species on the "fertile islands" under shrubs will profoundly change the nature and diversity of the native flora.

The mechanisms of the increases in density and biomass of the *Bromus* species are not readily apparent, but they appear to be related to their biological adaptations. They coincided with a series of years wetter than the 1951–1980 average for southern Nevada, which occurred from 1973 through 1988 (NOAA 1989). I have considered, but rejected, the hypothesis that the activities of man were the cause of the rapid increase in *Bromus* densities. Certainly the two species are well adapted to disturbance (Table 1), and man disturbs a great deal of the landscape. Nevertheless, the area disturbed by man on the NTS is not as great as that disturbed by burrowing animals and fires. Furthermore, the range extension for *B. tectorum* appeared to be widespread, and not restricted to the NTS (Young et al. 1987, Robertson 1987, Young and Tipton 1989). Disturbance by man, natural events, and animals is almost ubiquitous. Urban centers, grazing, use of off-road vehicles, and recreational use of public lands promise to maintain disturbance at high levels for the foreseeable future. The Nevada Test Site has been protected from some of those disturbances (grazing, residential development, and recreation) by the security required by the nuclear testing program. The spread of the *Bromus* species should therefore be considered a natural biological phenomenon.

ACKNOWLEDGMENTS

This work was supported by the U.S. Department of Energy under contract No. AC08-89NV10630. The Department of Energy, P. A. Medica, and T. L. Ackerman freely contributed historical data not otherwise available. The 1987–90 data were collected with capable field assistance from K. Dyka, C. E. Dull, and M. K. Lynch. The smut fungus was identified by Kalman Vanky. Useful suggestions for manuscript improvement were made by E. M. Romney, P. A. Medica, M. B. Saethre, K. L. Bowdridge,

R. M. Emanuel, G. E. Brown, and anonymous reviewers. I am grateful for the help of all those involved.

Literature Cited

Beatley, J. C. 1966. Ecological status of introduced brome grasses (*Bromus* spp.) in desert vegetation of southern Nevada. Ecology 47: 548–554.

______. 1976. Vascular plants of the Nevada Test Site and central-southern Nevada. Report TID-26881, National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia 22161. 308 pp.

Clokey, I. W. 1951. Flora of the Charleston Mountains, Clark County, Nevada. University of California Press, Berkeley. 274 pp.

Coville, F. V. 1893. Botany of the Death Valley Expedition. Contributions U.S. National Herbarium IV. 363 pp.

Ellner, S., and A. Shmida. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? Oecologia 51: 133–144.

Frenkel, R. E. 1970. Ruderal vegetation along some California roadsides. University of California Press, Berkeley. 163 pp.

Hunter, R. B. 1990. Recent increases in *Bromus* populations on the Nevada Test Site. Pages 22–25 *in* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller (compilers), Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-off, and other Aspects of Shrub Biology and Management. Intermountain Research Station, U.S. Department of Agriculture, Ogden, Utah 84401. 351 pp.

Hunter, R. B., and P. A. Medica. 1989. Status of the flora and fauna on the Nevada Test Site. U.S. Department of Energy Report DOE/NV/10630-2. National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia 22161. 103 pp.

Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. Theoretical Population Biology 26: 165–191.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7: 145–165.

Morrow, L. A., and P. W. Stahlman. 1984. The history and distribution of downy brome (*Bromus tectorum*) in North America. Weed Science 32 (suppl. 1): 1: 2–7.

Munz, P. A. 1974. A flora of Southern California. University of California Press, Berkeley. 1086 pp.

NOAA (National Oceanic and Atmospheric Administration). 1989. Climatological data annual summary. Nevada. Vol. 104(13). 31 pp.

O'Farrell, T. P., and L. A. Emery. 1976. Ecology of the Nevada Test Site: a narrative summary and annotated bibliography. Report NVO-167, U.S. Department of Energy. National Technical Information Services, U.S. Department of Commerce, 5285 Port Royal Road, Springfield, Virginia 22151. 249 pp.

Ostle, B. 1963. Statistics in research. 2d ed. Iowa State University Press, Ames. 585 pp.

Robertson, J. H. 1987. Here and there with Brome-tec [cheatgrass] (*Bromus tectorum*). Northern Nevada Native Plant Society Newsletter 13: 3–4.

Soholt, L. F., and W. K. Irwin. 1976. The influence of digging rodents on primary production in Rock Valley. US/IBP Desert Biome Research Memo 76-18. Utah State University, Logan. 10 pp.

Turner, F. B. 1972. Rock Valley validation site report. *In:* US/IBP Desert Biome Reports of 1971 Progress. Vol 3. 68 pp.

______. 1973. Rock Valley validation site report. US/IBP Desert Biome Research Memo 73-2. 211 pp.

Turner, F. B., ed. 1975. Rock Valley validation site report. US/IBP Desert Biome Research Memo 75-2. 53 pp.

______. 1976. Rock Valley validation site report. US/IBP Desert Biome Research Memo 76-2. 35 pp.

Turner, F. B., and J. F. McBrayer, eds. 1974. Rock Valley validation site. US/IBP Desert Biome Research Memo 74-2. 64 pp.

Yensen, D. I. 1981. The 1900 invasion of alien plants into southern Idaho. Great Basin Naturalist 41: 176–183.

Young, J. A., R. Evans, and S. Swanson. 1987. Snuff the candles in the desert. Northern Nevada Native Plant Society Newsletter 13: 3–4.

Young, J. A., and F. Tipton. 1990. Invasion of cheatgrass into arid environments of the Lahontan Basin. Pages 37–40 *in* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller (compilers), Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management. Intermountain Research Station, U.S. Department of Agriculture, Ogden, Utah 84401. 351 pp.

Received 30 October 1989
Revised 21 June 1990
Accepted 8 January 1991

Great Basin Naturalist 51(2), 1991, pp. 183–191

SIZE, AGE, AND DENSITY RELATIONSHIPS IN CURLLEAF MAHOGANY (*CERCOCARPUS LEDIFOLIUS*) POPULATIONS IN WESTERN AND CENTRAL NEVADA: COMPETITIVE IMPLICATIONS

Brad W. Schultz[1], R. J. Tausch[2], and Paul T. Tueller[3]

Abstract.—Size-density-age relationships in curlleaf mountain mahogany communities were studied in 25 study plots, each 30 × 30 m, in western and central Nevada. The influence of total vegetation cover (site potential) and relative mahogany cover (mahogany dominance) on the observed size-density-age relationships was investigated. A positive linear relationship was found between mean mahogany height and mean mahogany age. A positive nonlinear relationship was found between mean mahogany crown volume and mean mahogany age. Negative nonlinear relationships were found between mean mahogany density and mean mahogany age, and mean mahogany density and mean mahogany crown volume. Strong negative relationships were fonnd between the mean combined density of established seedlings, juvenile, and immature mahogany and mean mahogany age and mean mahogany crown volume. Including total cover in the regression relationships between size, age, and density never increased the r^2 value by more than .05. The addition of relative mahogany cover improved the r^2 value for the relationship between mean mahogany density and mean mahogany crown volume by .28. The strong size-density and age-density relationships found indicate that intraspecific competition is probably occurring in the communities sampled, and that established seedlings, juvenile, and immature plants are the first individuals affected. Direct tests are needed to confirm these relationships.

Key words: curlleaf mahogany, size-age-density relationships, intraspecific competition, population dynamics.

An understanding of the relationships between size, density, and age in a plant population is key to understanding the processes of intraspecific competition and population dynamics (Westoby 1977, 1981, Harper 1977). These relationships can be studied based on either the individuals of a species on one site over time or data from a series of different sites of different ages. Because curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt. T & G) is a slow-growing, long-lived species, the latter method was used.

Relationships between population variables of size, density, and age can be used as indicators of a population's dynamics (Harper 1977). One example is the general relationship between average plant size and the density of a species fully occupying a site. This size-density relationship has been widely represented by the allometric equation $Y = kP^a$ (White 1981, Long and Smith 1984, Westoby 1984, and Westoby and Howell 1986) where Y is mean plant size, P is plants per unit area, and a and k are constants. When plant populations reach full site occupancy, the maximum size-density relationship possible for that site has been obtained and density reductions occur (Hutchings and Budd 1981).

The size-density relationship has been broadly applied to many types of plants but not always consistently (Weller 1987, 1989, Zeide 1987). There have also been questions about the statistical validity of the relationship, in particular the possibility of specious correlation (Weller 1987). It has been shown in a review of the procedures by Prairie and Bird (1989) that most of the questions regarding statistical validity have resulted from misconceptions about the relationship. They provide criteria supporting these types of analyses.

Models based on size-density relationships have been used to provide a base from which to evaluate the competitive interactions between the individuals in a population (Hutchings and Budd 1981, Long and Smith 1984,

---

[1] Department of Range, Wildlife and Forestry, University of Nevada, Reno, Reno, Nevada 89512. Present address: Environmental Sciences Department, EG&G Energy Measurements, Inc., Box 1912, M/S P-03, Las Vegas, Nevada 89125.

[2] USDA Forest Service, Intermountain Forest and Range Experiment Station, Reno, Nevada, 89512.

[3] Department of Range, Wildlife and Forestry, University of Nevada, Reno, Reno, Nevada 89512.

Gaudet and Keddy 1988). Drew and Flewelling (1979) have demonstrated the practical application of the use of a size-density model in the analysis and management of stand density in Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco) plantations. Size-density models have also been successfully used in stand growth models (Smith and Hann 1984, Lloyd and Harms 1986, Smith 1986).

Most research on plant competition has centered on a phenomenological nonpredictive approach (Gaudet and Keddy 1988). Additional progress requires a predictive approach that allows general principles to be deduced that apply beyond the species and conditions of a particular site or study. Gaudet and Keddy (1988) have shown that plant biomass, plant height, canopy diameter, canopy area, and leaf shape explain most of a plant's competitive ability.

Information on intraspecific competition as related to relationships between size, age, and density in curlleaf mahogany communities is nonexistent. The first objective of this study was to quantify size, age, and density relationships in selected curlleaf mahogany populations. The second objective was to describe possible reasons for the observed size-age-density relationships. Explanations for the often-noted poor recruitment (Scheldt and Tisdale 1970) of new individuals into mature curlleaf mahogany stands were also explored.

STUDY SITE DESCRIPTIONS

Curlleaf mahogany communities were sampled in 25 study plots on three mountain ranges in western (Peavine Mountain: 9 plots, Carson Range: 4 plots) and central (Shoshone Range: 12 plots) Nevada during May–August 1985.

On Peavine Mountain scattered mahogany occur near 1890 m on west, east, and north aspects but dominate stands only above 1980 m. Mahogany stands on south-facing slopes are found above 2260 m. Individual stands vary in size from 1 to over 300 ha. Smaller stands are most common along rocky ridges and as islands within low sagebrush (*Artemisia arbuscula* Nutt.) communities. Large stands occur on hillsides and are commonly surrounded by mountain big sagebrush (*Artemisia tridentata* var. *vaseyana* [Rydb.] J. Boivin) communities. Annual precipitation averages 36–41 cm and occurs mostly as snow. The average frost-free period is 50–80 days. Curlleaf mahogany is largely restricted to the Ticino gravelly fine sandy loam (SCS 1983), with an effective rooting depth of 51–103 cm.

Sampling on the Carson Range occurred in mahogany stands between 1550 and 1890 m. The mixed conifer zone generally occurs above 1900–2000 m. Individual mahogany stands vary in size and tree density as on Peavine Mountain. Average annual precipitation is 36–51 cm and occurs mostly as snow during the winter months. The average frost-free period is 50–80 days. Soils supporting mountain mahogany are Duckhill stony loam, Apmat gravelly sandy loam, and the Fraval-Hirschdale-Jumbo association (SCS 1983). Effective rooting depth varies from 51 to over 154 cm.

Mahogany on the Shoshone Range occur as low as 2150 m on north aspects, but large stands are rarely present below 2380 m. Southern aspects have few mahogany stands below 2600 m. All other aspects have abundant mahogany stands between 2450 and 3050 m. Limber pine (*Pinus flexilis* James) is a common associate above 2900 m. Stand size is variable, ranging from less than 1 to over 300 ha. Smallest stands occur along rocky ridge lines, and largest stands on sloping mountain sides and in bowls below the mountain crest. Annual precipitation averages 41–51 cm; but unlike western Nevada, heaviest precipitation normally occurs early in the growing season (March–June), and summer rainfall is slightly more abundant (Hougton et al. 1975). The frost-free period is 50–80 days. Mountain mahogany tends to be restricted to the Fox mount soil series, specifically Foxmount gravelly loam (Carol Jett, personal communication). These soils are well drained, moderately permeable, and have an effective rooting depth of 51–103 cm.

Average understory cover in each study area is almost identical (14–15%) (Schultz et al. 1990). Average vegetative cover on the Shoshone Range (98%) is substantially greater than on Peavine Mountain (70%) and the Carson Range (68%) (Schultz et al. 1990). A similar relationship for average curlleaf mahogany cover is also present: Shoshone Range 79%, Peavine Mountain 56%, and Carson Range 54% (Schultz et al. 1990).

TABLE 1. Mountain mahogany maturity classes developed from a reconnaissance of mahogany stands near Reno, Nevada.

1. Established seedling	young plants; 2–7 mm basal diameter; smooth bark; plants may be up to 30 cm in height
2. Juvenile	young plants greater than 7 mm basal diameter; smooth bark; plants to 60 cm tall
3. Immature	young plants greater than 1.25 cm basal diameter; smooth bark; plants to 1.5 m tall
4. Young-mature	cracked bark; 1.5–3.0 m tall; crown broadened; may be multistemmed from base; not suppressed
5. Mature	cracked bark; wide full crown; few dead branches; may have several stems from base; may be suppressed; greater than 3 m tall
6. Overmature	cracked bark; may be multistemmed; numerous dead branches; may be greater than 3 m tall; frequently suppressed

METHODS

Field Sampling

An initial field reconnaissance near Reno, Nevada, indicated that mahogany stands are composed of individuals categorized into six maturity classes: established seedling, juvenile, immature, young-mature, mature, and overmature (decadent) (Table 1).

Sampling occurred in 30 × 30-m study plots, each having at least one young-mature individual and placed as close to a cardinal aspect as permitted by access and mahogany distribution. Ecotones with adjacent plant communities were avoided. Upper, middle, and lower portions of the mahogany belt were sampled when the elevation range exceeded 500 m.

Mahogany density and maturity class distribution were recorded in each study plot (density/900 m^2). All mahogany plants, except established seedlings, were measured to obtain crown diameters (the two longest perpendicular diameters) and height. Established seedlings had only crown measurements recorded on plants selected for growth ring analyses.

Crown measurements were used to calculate mahogany cover (%) and mahogany crown volume (m^3) (Ludwig et al. 1975, Tausch 1980). All measurements were of the green leaf portion of the canopy and were made to the nearest decimeter (dm).

Four randomly selected individuals from each maturity class present in each study plot were cut to estimate plant age. Relative growth rates (RGR), using growth ring widths (Davis et al. 1972, Brotherson et al. 1980), were also determined on each cross section. If a maturity class had less than four individuals present, all plants were cut for age and growth ring analysis. Cross sections were cut as close to the ground as possible, and from the largest living stem.

Understory vegetation within each study plot was sampled in three randomly located 30-m belt transects (Schultz et al. 1990). Cover was occularly estimated in 15 shrub quadrats (1 × 2 m) and 30 grass and forb quadrats (20 × 50 cm). Crown cover (%) was estimated for shrub and forb species, and basal area (%) for grasses. The density of current-year mahogany seedlings (density/m^2) was also recorded in each 1 × 2-m quadrat. Current-year seedlings usually had 4–8 leaves and were less than 2.5 cm tall.

Data Analysis

Crown diameter, crown height, and crown area (m^2) were computed for each tree measured. Total crown area and total crown cover (%) values were calculated for each maturity class and study plot by summing the area occupied by individual plants. Average values were determined on each study area.

Relative mahogany cover (mahogany cover divided by total study plot cover) was calculated for each study plot and study area. Crown volume (m^3) was computed for each mahogany plant using the formula for one-half of an ellipsoid (Tausch 1980). Total and mean values for each maturity class, study plot, and study area were calculated.

Mahogany density (density/900 m^2) was determined for each study area. Growth ring counts and measurements from the mahogany subsample were made along two sanded radii on each cross section. Growth rings were identified by a single row of relatively large vessels in the springwood (Schultz et al. 1990). Modifications of a technique using acetic acid and zinc oxide (Parker et al. 1976) were used to enhance the contrast between early- and latewood in each annual ring. Time and funding constraints did not allow us to determine whether false rings were present. Reference chronologies were not available for cross dating.

Yearly growth increments were measured to the nearest 0.01 mm for the 10 years before harvest using a Craighead-Douglas dendrochronograph and a binocular microscope. Age and ring width data from the two radii were averaged to determine a mean value for each cross section. Age data were considered reliable when values from the radii were within 5% of each other. Ring width data were used to calculate the mean stem area increment ([MSAI] [cm^2/10 years]) of each cross section (Schultz et al. 1990). Mean age, ring width, and MSAI values were summarized for each maturity class in each study area. Estimated mean age values for all maturity classes were based on the subsampled trees. Mean study plot age values were calculated by weighting the mean value of each maturity class by its density, summing, and dividing by total plot density. Study plot means were averaged for mean study area values. Relationships between age and size were not computed for the individual mahogany in each study plot because of the subsampled age data.

Age is an important predictor of a plant's fate only insofar as it affects plant size (Westoby and Howell 1986). Size is considered the primary determinant of survival (Westoby and Howell 1986). Each of the areas we sampled had mahogany stands composed of individuals of various size and age. To focus the analyses on the full range of variation sampled, we pooled data from all three sites.

All analyses of size, age, and density were first done using linear regression techniques. The residuals from these analyses were used to determine which were nonlinear. Nonlinear relationships were then analyzed using an iterative nonlinear regression technique to fit the data to the equation $Y = aX^b$ (Caceci and Cacheris 1984), where Y is mountain mahogany density or size, X is mean mahogany age or mean mahogany crown volume, and a and b are constants. This avoided the problems associated with logarithmic transformation of the data for analysis (Payendeh 1981, Brand and Smith 1985).

Following the completion of simple linear and nonlinear regression analyses, multiple linear ($Y = a + bX + cZ$) and nonlinear ($Y = aX^bZ^c$) analyses were performed. Values for total vegetation cover and relative mahogany cover were used for Z in these analyses. These analyses provide an indication of how site potential (total plant cover) and dominance by mahogany (relative mahogany cover) in the sampled plots affected the size-age-density relationships observed. Methods for independent site potential estimates needed for direct tests of these relationships are not available for mahogany woodlands. Values for total vegetation cover, relative mahogany cover, and nonmahogany cover are from Schultz et al. (1990). The r^2 values for nonlinear analyses were computed according to the methods of Brand and Smith (1985). This r^2 has the same interpretation (% of variation in Y explained by variation in X) as for linear regression. The significance level is $P < .05$ or greater for all linear regression analyses. Significance levels are not directly available for nonlinear regression. Significance levels for the equivalent analyses using logarithmically transformed data were $P < .05$ or better.

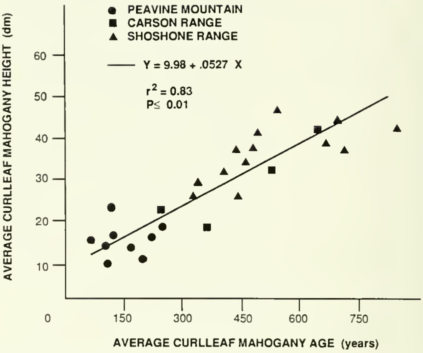


Fig. 1. Major landforms and vegetative communities on the NTS as determined by Beatley (O'Farrell 1976).

RESULTS

Size-Age-Density Relationships

The relationship between average mahogany height and average mahogany age was the only one found to be linear (Fig. 1). The older the average age of the mahogany in a stand, the greater the average height. Including total cover in a multiple linear regression improved the results,

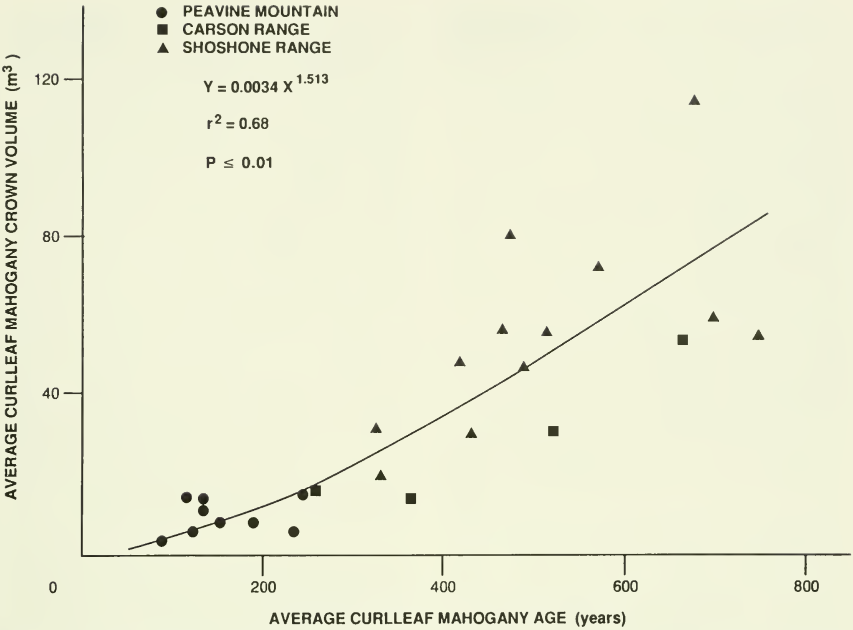


Fig. 2. Nonlinear relationship between average curlleaf mahogany crown volume (m^3) and average curlleaf mahogany age (years) for three sites in Nevada.

$$Y = 2.71 + 0.0449X + 0.121Z, r^2 = .86, P < .001 \quad (1)$$

where Y is average mahogany height (dm), X is average mahogany age (years), and Z is the total vegetal cover (%) of the plots. The contribution of Z was significant ($P < .05$). Sites with higher total plant cover (%) tended to have taller mahogany for a given age than sites with lower total vegetal cover. This seems consistent with total cover representing site potential.

Average mahogany crown volume increased with average mahogany age (Fig. 2). Including total plant cover or relative mahogany cover for Z in a multiple nonlinear regression analysis increased the r^2 by less than .01 over that in Figure 2. The increase in mahogany crown volume with increasing stand age did not appear to be affected by either total plant cover or level of mahogany dominance in the sampled plots.

Average mahogany density had a strong nonlinear relationship with average mahogany age (Fig. 3). Including total plant cover or relative mahogany cover for Z in a multiple nonlinear regression analysis increased the r^2 by less than .01 over that in Figure 3. The decrease in mahogany density with increasing stand age for the sampled stands was independent of both total plant cover and mahogany dominance.

Mahogany density was highest in study plots that had an average age of less than 150 years, but it was substantially lower in study plots that had an average age of 250–300 years. Study plots with a mean age beyond 300 years had similar densities.

The density of established seedling, juvenile, and immature maturity classes had a similar, but steeper, negative relationship to average mahogany age as in Figure 3,

$$Y = 103428X^{-1.486}, r^2 = .81 \quad (2)$$

where Y is the density of established seedling, juvenile, and immature mahogany (density/900m^2), and X is average mahogany age

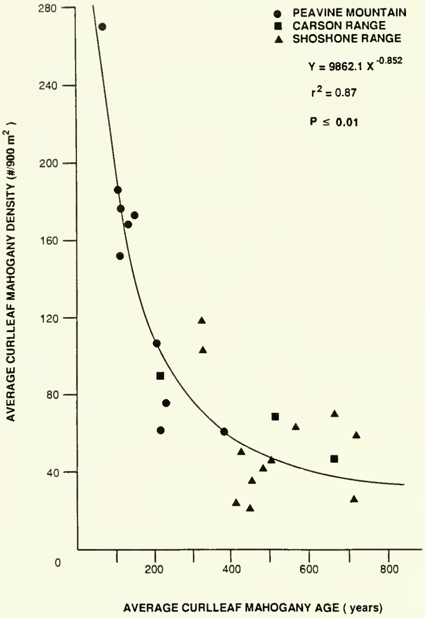


Fig. 3. Nonlinear relationship between average curlleaf mahogany density (#/900 m^2) and average curlleaf mahogany age (years) for three sites in Nevada.

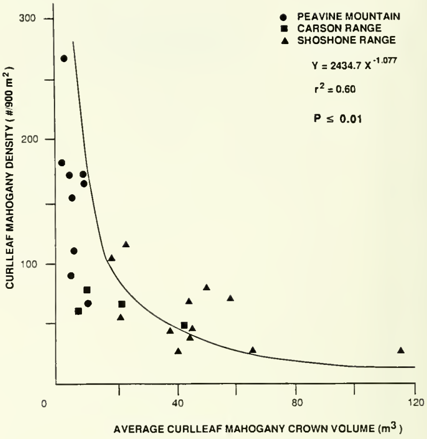


Fig. 4. Nonlinear relationship between average curlleaf mahogany crown volume (m^2) and curlleaf mahogany density (#/900 m^2) for three sites in Nevada.

(years). The addition of total plant cover (Z) to the relationship in Equation 2 had the greatest improvement on r^2, but the improvement was less than .02.

Mahogany density had an inverse nonlinear relationship with average mahogany crown volume (Fig. 4). Including relative mahogany cover for Z in a multiple nonlinear analysis improved the relationship,

$$Y = 0.0213X^{-1.48}Z^{3.051},\ r^2 = .88 \qquad (3)$$

where Y is mahogany density (density/900m^2), X is average curlleaf mahogany crown volume (m^3), and Z is relative mahogany cover (%). For the same density, sites with higher mahogany dominance (relative mahogany cover) had larger plants than sites with lower mahogany dominance. The indication is that there may be a relationship between site potential and the ability of a given density of mahogany to dominate a site. The better the site, the larger the individual plants can become. An independent measure of site potential would be necessary to directly test this.

The density of reproduction, juvenile, and immature maturity classes had a similar, but steeper, negative nonlinear relationship with average crown volume as in Figure 4,

$$Y = 505X^{-1.15},\ r^2 = .78 \qquad (4)$$

where Y is the density of reproduction, juvenile, and immature mahogany (#/900m^2), and X is average mahogany crown volume (m^3). The addition of either mahogany or nonmahogany cover did not improve the relationship. The negative effect of large mahogany on mahogany seedlings appears generally independent of the relative levels of mahogany and nonmahogany cover. However, the addition of total plant cover (%) for Z improved the relationship:

$$Y = 0.510X^{-1.27}Z^{1.69},\ r^2 = .83. \qquad (5)$$

For stands with the same mean mahogany crown volume, the density of young mahogany tended to be slightly higher on plots with higher total cover. This may be a reflection of better site conditions somewhat offsetting the suppression of the younger mahogany by the dominant individuals. This possibility needs additional study.

DISCUSSION

Strong size, age, and density relationships were present in the mountain mahogany communities sampled (Figs. 1–4). Stands on Peavine Mountain, the Carson Range, and the Shoshone Range appeared to follow the same general trend. Relatively early in stand development (mean mahogany age less than 250–300 years) increases in mahogany size are accompanied by sharp declines in stand density. The change in the slope of the regression line that occurred beyond an average mahogany age of 250–300 years coincides with mahogany communities dominated by large, mature individuals (Schultz et al. 1990). These sites were mostly in the Shoshone Range. After mean mahogany age exceeded 300 years, mahogany density continued to decline with increasing stand age, but the rate of decline was reduced.

As mahogany stands increase in average age, average canopy volume and height of the individuals present increase (Figs. 1, 2, Schultz et al. 1990). As average canopy height and volume increase, stand density declines (Fig. 4, Eq. 3). This increase in plant size, together with a concomitant decrease in plant density with age, reflects the size-density relationships reported for many plant populations (Harper 1977).

Eventually, increases in individual plant size cause interference between individual plants and competition for essential resources (Hutchings and Budd 1981). As growth continues, a point is eventually reached where the habitat can support no additional biomass. Further growth can occur only when mortality occurs among existing plants. The strong size-density and age-density relationships present in Figure 4 and Equation 2, respectively, indicate that competition is probably occurring in the mountain mahogany communities sampled. Total stand density declines sharply as mean plant size increases. The density of the youngest individuals also declines, but more rapidly, as average mahogany age increases.

Gaudet and Keddy (1988) have shown that plant biomass explains a substantial part of a plant's competitive ability. Plant height, canopy diameter, canopy area, and leaf shape explain most of the residual variation. Biomass was not measured in this study, but volume measurements can be substituted for biomass, since studies have shown that volume and biomass are isometrically related (White 1981). Figure 4 indicates that average curlleaf mahogany crown volume, hence biomass, has a strong negative relationship with stand density. Average stand age, in itself, has no influence on a stand's population dynamics. As stands age, however, physical dimensions, such as average crown volume, average biomass, and average crown diameter, increase; and these physical attributes undoubtedly influence competitive interactions.

The inverse relationship of mahogany density and average mahogany crown volume (Fig. 4) was improved substantially by including relative mahogany cover (mahogany dominance) in the analysis (Eq. 3). This situation is similar to data reported by Gaudet and Keddy (1988). In their work plant height, canopy diameter, and canopy area further explained a plant's competitive ability beyond biomass alone.

A reduction of growth rates in individual plants relative to their potential can be an indication of plant competition (Long and Smith 1984). Relative growth rates, as represented by average ring width (mm), and mean stem area increment [(MSAI) (cm^2/10 yr)] for each study plot for the last 10 years are reported in Schultz et al. (1990). Mountain mahogany stands on Peavine Mountain had the greatest RGR, as represented by average ring width and MSAI. If ring width and MSAI values on Peavine Mountain are assumed to be the maximum potential growth rates obtainable by curlleaf mahogany, then the RGRs in the Carson and Shoshone ranges are substantially reduced relative to the species' potential. This occurred despite similar soils and climate.

Previous work (Schultz et al. 1990) found that mean mahogany size and total mahogany crown volume are significantly ($P \leq .05$) less on Peavine Mountain than on the Carson and Shoshone ranges. Because larger individuals have a competitive influence considerably beyond what is proportional to their size (Bella 1971), it is likely that intraspecific competition is greatest in Carson and Shoshone ranges.

Since mahogany size is a function of stand age (Figs. 1, 2), we interpret the greater steepness of the regression lines in Equations 2 and 5 compared with Figure 3 to imply that established seedling, juvenile, and immature mahogany are the first individuals in a stand affected by increasing mahogany size and, therefore, intraspecific competition. If intraspecific competition affected individuals of all sizes equally, the slope of the regression lines for all three analyses would be similar. Other research (Bella 1971, Weiner 1984, Grace 1985) has shown that the youngest and smallest individuals present in a population are the plants most affected by intraspecific competition. Schultz et al. (1990) found that Peavine Mountain has a population structure in which 62% of the plants present were from the established seedling, juvenile, and immature maturity classes. In contrast, the Carson and Shoshone ranges, respectively, had 9 and 18% of their population structure composed of individuals from these maturity classes. Mean mahogany crown volume on Peavine Mountain was 3.4 and 6.8 times smaller than on the Carson and Shoshone ranges, respectively.

As mean mahogany size continues to increase, few, if any, established seedling, juvenile, and immature mahogany are left. This situation is similar to other studies that have noted poor or absent reproduction as an indicator of competition (Long and Turner 1975, Oliver 1981).

The often-noted poor recruitment of new mahogany into mature stands can probably be explained, to some degree, by the size-density relationships observed. Data on estimated population growth rates (Schultz et al. 1990) show that mahogany communities with large average crown volumes (Shoshone and Carson ranges) have had slow population growth rates since the oldest individuals were established 500 or more years ago. Where average crown volume is relatively small (Peavine Mountain), established seedling, juvenile, and immature mahogany are abundant, and the population size has increased steadily since the oldest individuals became established.

Mahogany communities with small average crown volumes have comparatively lower mahogany cover (Schultz et al. 1990). Low mahogany cover increases the incidence of canopy gaps, which appear to be essential for the recruitment of young mahogany into the population (Schultz et al. 1990). Canopy closure has been found to indicate competition is occurring (Assman 1970). Mahogany cover in the Shoshone Range averaged 79%, but it approached or exceeded 100% in almost half the study plots sampled. In study plots with less than 100% mahogany cover the spatial structure of the community is such that mahogany thickets with cover greater than 100% are common (personal observation). The Carson Range has a similar structural appearance.

Low densities of established seedling, juvenile, and immature mahogany can also be due to a lack of viable seed, poor seedling establishment, or poor recruitment of established seedlings into successively older maturity classes. Lack of viable seed did not appear to be a problem, since the Shoshone Range had a current-year seedling density of $2.0/m^2$. Personal observation indicates that stands with high mahogany cover and large average crown volumes have deep and persistent litter cover. Deep plant litter probably limits mahogany seedling survival and establishment (Schultz et al. 1990). Seedlings rooted in deep litter frequently do not have their roots established in mineral soil, and as soon as the litter material dries out the seedlings become dessicated and die (personal observation). Marquis et al. (1964) and Keever (1973) have observed that the establishment of relatively small-seeded species is adversely affected by continuous litter cover.

CONCLUSIONS

Curlleaf mountain mahogany stands composed of large, mature individuals have lower total stand densities and lower densities of established seedling, juvenile, and immature mahogany. Over time intraspecific competition apparently occurs and probably intensifies as a result of increasing plant size. Intraspecific competition reduces the growth rates of all maturity classes below the potential growth rates for the species. Competition also appears to increase mortality in the smallest individuals present. This explains the often-noted poor recruitment (Scheldt and Tisdale 1970) of new individuals into mature mahogany stands. Increased mortality in the smallest and youngest individuals results in a maturity class structure dominated by relatively few, but very large, mature individuals. The plentiful establishment of young mahogany is probably not possible unless stands composed of large, mature trees have their canopies opened up, and intraspecific competition is reduced.

LITERATURE CITED

ASSMAN, E. 1970. The principles of forest yield studies. Studies in the organic production, structure increment, and yield of forest stands. Pergamon Press, Oxford.

BELLA, I. E. 1971. A new competition model for individual trees. Forest Science 17: 364–372.

BRAND, G. J., AND W. B. SMITH. 1985. Evaluating allometric shrub biomass equations fit to generated data. Canadian Journal of Botany 63: 64–67.

BROTHERSON, J. D., J. N. DAVIS, AND L. GREENWOOD. 1980. Diameter-age relationships of two species of mountain mahogany. Journal of Range Management 33: 367–370.

CACECI, M. S., AND W. P. CACHERIS. 1984. Fitting curves to data. Byte 9: 340–362.

DAVIS, J. B., P. T. TUELLER, AND A. D. BRUNER. 1972. Estimating forage production from shrub ring widths in Hot Creek Valley, Nevada. Journal of Range Management 24: 398–402.

DREW, T. J., AND J. W. FLEWELLING. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. Forest Science 25: 518–532.

GAUDET, C. L., AND P. A. KEDDY. 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334: 242–243.

GRACE, J. B. 1985. Juvenile vs. adult competitive abilities in plants: size-dependence in cattails (Typha). Ecology 66: 1630–1638.

HARPER, J. L. 1977. The population biology of plants. Academic Press, New York.

HOUGHTON, J. G., C. M. SAKAMOTO, AND R. O. GIFFORD. 1975. Nevada's weather and climate. Special Publication 2. Nevada Bureau of Mines and Geology.

HUTCHINGS, M. J., AND C. S. J. BUDD. 1981. Plant self-thinning and leaf area dynamics in experimental and natural monocultures. Oikos 36: 319–325.

KEEVER, K. 1973. Distribution of major forest species in southern Pennsylvania. Ecological Monographs 43: 303–327.

LLOYD, F. T., AND W. R. HARMS. 1986. An individual stand growth model for mean plant size based on the rule of self-thinning. Annals of Botany 57: 681–688.

LONG, J. N., AND F. W. SMITH. 1984. Relation between size and density in developing stands: a description and possible mechanisms. Forest Ecology Management 7: 191–206.

LONG, J. N., AND J. TURNER. 1975. Aboveground biomass of understory and overstory in an age sequence of four Douglas-fir stands. Journal of Applied Ecology 12: 179–188.

LUDWIG, J. A., J. F. REYNOLDS, AND P. D. WHITSON. 1975. Size biomass relationships in several Chihuahuan Desert shrubs. American Midland Naturalist 94: 451–461.

MARQUIS, D. A., J. C. BJORKBOM, AND G. YELENOSKY. 1964. Effects of seedbed condition and light exposure on paper birch regeneration. Journal of Forestry 62: 876–881.

OLIVER, C. D. 1981. Forest development in North America following major disturbances. Forest Ecology Management 3: 153–168.

PARKER, M. L., G. M. BARTON, AND J. H. G. SMITH. 1976. Annual ring contrast and enhancement without affecting X-ray densitometer studies. Tree Ring Bulletin 36: 29–31.

PAYANDEH, B. 1981. Choosing regression models for biomass equations. Forest Chronicle 57: 229–232.

PRAIRIE, Y. T., AND D. F. BIRD. 1989. Some misconceptions about the spurious correlation problem in the ecological literature. Oecologia 81: 285–288.

SCHELDT, R. S., AND E. W. TISDALE. 1970. Ecology and utilization of curlleaf mountain mahogany in Idaho. University of Idaho, Forest, Wildlife, and Range Experiment Station Note 15.

SCHULTZ, B. W., P. T. TUELLER, AND R. J. TAUSCH. 1990. Ecology of curlleaf mahogany (*Cercocarpus ledifolius*) in western and central Nevada: community and population structure. Journal of Range Management 43: 13–20.

SCS. 1983. Soil Survey of Washoe County, Nevada. Southern part. USDA, Washington, D.C.

SMITH, N. J. 1986. A model of stand allometry and biomass allocation during the self-thinning process. Canadian Journal of Forest Research 14: 605–609.

SMITH, N. J., AND D. W. HANN. 1984. A new analytical model based on the −3/2 power rule of self-thinning. Canadian Journal of Forest Research 14: 605–609.

TAUSCH, R. J. 1980. Allometric analysis of plant growth in woodland communities. Unpublished dissertation, Utah State University, Logan.

WEINER, J. 1984. Neighborhood interference amongst *Pinus rigida* individuals. Journal of Ecology 72: 183–196.

WELLER, D. E. 1987. A reevaluation of the −3/2 power rule of plant self-thinning. Ecological Monographs 578: 23–42.

______. 1989. The interspecific size-density relationship among crowded plant stands and its implications for the −3/2 power rule of self-thinning. American Naturalist 133: 20–41.

WESTOBY, M. 1977. Self-thinning driven by leaf area not by weight. Nature 26: 330–331.

______. 1981. The place of the self-thinning rule in population dynamics. American Naturalist 118: 581–587.

______. 1984. The self-thinning rule. Advances in Ecological Research 14: 167–225.

WESTOBY, M., AND J. HOWELL. 1986. Influence of population structure on self-thinning of plant populations. Journal of Ecology 74: 343–359.

WHITE, J. 1981. The allometric interpretation of the self-thinning rule. Journal of Theoretical Biology 89: 475–500.

ZEIDE, B. 1987. Analysis of the −3/2 power law of self-thinning. Forest Science 33: 517–537.

Received 30 March 1991
Revised 8 January 1991
Accepted 28 March 1991

Great Basin Naturalist 51(2), 1991, pp. 192–197

FIELD ACETYLENE REDUCTION RATES OF *LUPINUS ARGENTEUS* ALONG AN ELEVATIONAL GRADIENT[1]

M. D. Rumbaugh[2] and D. A. Johnson[2]

ABSTRACT.—The effects of elevation and environmental parameters associated with elevation on the dinitrogen fixation rates, $N_2[C_2H_2]$, of a North American lupine species were evaluated. *Lupinus argenteus* Pursh plants growing at five elevations on Francis Peak, Utah, were sampled weekly throughout the growing season. The highest elevation site had the greatest frequency of nodulated plants. Influence of the environmental and physiological variables on fixation activity varied with elevation and the mean time of sampling. Soil moisture, nodule dry weight, and air temperature were important. Less than one-half of the observed variation in fixation rates, $N_2[C_2H_2]$, was accounted for by variation in the associated independent variables. Nevertheless this study documented that nodulated plants of *L. argenteus* were capable of actively fixing nitrogen at a range of elevations on Francis Peak.

Key words: ecology, ecophysiology, legume, nitrogen fixation, nodulation, rangeland, Rhizobium lupini.

Species of *Lupinus* are found from timberline to seacoast in much of the western United States (Phillips 1955). Their importance in the nitrogen economy of range ecosystems has not been extensively investigated. Native legumes are believed to supply biologically fixed nitrogen to the semiarid rangeland plant communities in which they occur, but their role has not been well documented (Farnsworth et al. 1978). Johnson and Rumbaugh (1981) studied the acetylene reduction rates, $N_2[C_2H_2]$, of nodules of 34 legume species growing on mountain grassland sites, big sagebrush–dominated sites, and cultivated former big sagebrush sites in northern Utah. Nodules were present and active in some species even during the driest part of the growing season. However, 13 of the 17 species of lupines native to North America that were growing in a cultivated nursery environment were not nodulated even though the seeds had been inoculated with a commercial peat-base inoculum.

Pegtel (1980) investigated *Lupinus laxiflorus* Dougl., *L. lepidus* Lindl., and *L. polyphyllus* Lindl. on undisturbed sites with serpentine and nonserpentine soils on Mt. Stuart in the Wenatchee Mountains of Washington. All root systems had nodules, and serpentine and nonserpentine populations had the same number of nodules per plant. Additional laboratory research showed that the wild strains of *Rhizobium lupini* all fixed atmospheric nitrogen but that their effectiveness was variable and generally lower than commercially available strains. *L. polyphyllus* had a higher effectivity of nodulation than *L. argenteus* and *L. lencophyllus* in a greenhouse study (Walsh et al. 1983).

McNabb and Geist (1979) measured nitrogen fixation rates ranging from 1 to 10 kg N/ha for four perennial *Lupinus* species native to the Pacific Northwest. There was a significant seasonal variation in nodule biomass of two of the species. The potential for lupine nitrogen fixation was believed to be dependent primarily on nodule biomass. Similarly, whole plant estimates of nitrogen fixation by high-altitude legumes in Montana and Utah were 5 to 15 times greater for *L. argenteus* than for native *Astragalus* and *Trifolium* species (Johnson and Rumbaugh 1986). The difference was ascribed to the greater nodule mass of the lupine.

The objective of this study was to assess the effects of changes in elevation and environmental parameters associated with elevation on nitrogen fixation rates of a native lupine species growing on a semiarid mountain rangeland in the intermountain region of the western United States.

---

[1] Cooperative investigations of the USDA–Agricultural Research Service and the Utah Agricultural Experiment Station, Logan, Utah 84322. Approved as Journal Paper No. 4105.

[2] USDA–Agricultural Research Service, Forage and Range Research Laboratory, Utah State University, Logan, Utah 84322-6300.

SITE DESCRIPTIONS AND METHODS

The five study sites were located on west or northwest aspects of Francis Peak in the Wasatch Range of north central Utah. All were within or adjacent to the Davis County Experimental Watershed, which was established in 1930 as a United States Forest Service–administered research area. The climate and vegetation of the watershed is generally representative of a large part of the low- to mid-elevation (1500 to 2800 m) mountain country in the intermountain area. Summers are short, cool, and dry. Most summer storms are convective thundershowers of less than six hours duration (Farmer and Fletcher 1971). The highest average annual precipitation of 1043 mm occurs on the upper part of the watershed. Soil moisture depletion begins immediately after snowmelt and continues to increase at a rapid rate into July (Johnston and Doty 1972). Lupines are most common on Cryoboroll soils with slopes of 8 to 30%. Associated species include *Agropyron cristatum* (L.) Gaertn., *Artemisia tridentata* Nutt., *Bromus carinatus* H. & A., *Carex* sp., *Chrysothamnus nauseosus* (Pall.) Britt., *Madia glomerata* Hook., and *Symphoricarpos* sp.

Study sites with adequate numbers of *L. argenteus* plants for sampling throughout the growing season were selected at five elevations. These populations were located at mean elevations of 1478, 2027, 2256, 2454, and 2713 m. Vegetation along the elevational gradient varied from a desert shrub association near the base of the mountain to a subalpine meadow at the highest site. One to five representative plants were chosen at approximately weekly intervals at each elevation throughout the growing season. Sampling began on 4 June 1980 at the lowest elevation and was terminated on 21 October 1980 at the highest elevation.

Leaf water potential was measured on each plant by standard pressure chamber techniques (Scholander et al. 1965), the shoot was cut at the soil level for dry biomass weight, and the root system was excavated. Excised root segments with attached nodules were used for the acetylene reduction procedures. The techniques described by Waughman (1971) and used by Westermann and Kolar (1978) and Johnson and Rumbaugh (1981) were followed with the exception of limiting the incubation period to one hour. The hour of sampling was recorded as well as the numerical day of the calendar year. Sampling was limited to the hours between 10:00 a.m. and 4:00 p.m. each day. Care was exercised to shield exposed nodules and incubation chambers from direct sunlight. Air temperature was measured with a mercury thermometer and soil temperature with a bimetallic dial thermometer with a 10-cm probe. Soil samples for moisture determinations were collected from 0–20 cm and 20–40 cm depths.

RESULTS AND DISCUSSION

Air and soil temperatures tended to be lower at the higher sites along the gradient (Table 1). Soil moisture throughout the depth of the profile tested was higher at the 2713-m site than at the four lower elevations. The 1478-m area was situated on a west-facing slope, and soils at this site were deeper than at the other locations. The lupine plants had large, woody tap roots, and nodules were located only on lateral roots. The study area at 2027 m sloped sharply toward the south and was shaded a considerable part of the day by the mountain peak. This location also was the only one of the five sites with trees that shaded the lupine plants. These shading factors probably resulted in the soil temperatures being lower than for sites immediately higher and lower on the mountain side. The 2256-m elevation appeared to be the most xeric of all the study areas. Lupines were growing intermixed with a dense population of *Artemisia tridentata*. The soils at the 2454- and 2713-m elevation sites were shallow and rocky. *L. argenteus* grew in almost pure stands with only a few plants of other forbs as associated species. Plants at the highest site were more uniform in size than at lower elevations, they had less-extensive root systems, and it was easier to find nodules than at the other four study areas.

Plants at the extreme elevations were smaller than those at intermediate elevations (Table 1). Shoot weight was more closely associated with soil moisture than with mean temperatures. The simple correlation of aboveground plant weight with soil moisture in the 20–40 cm zone was $r = -.27$ ($P < .01$). All other coefficients were of lower magnitude. Shoot weight was positively associated

Table 1. Environmental and physiological variables measured at five sites on Francis Peak, Utah, during 1980. Acetylene reduction activity, $N_2[C_2H_2]$, of nodulated *Lupinus argenteus* plants is expressed as µ moles of ethylene/h/g nodule fresh weight.

	Site elevation (m)						
Variable	1478	2027	2256	2454	2713	Variable mean	L.S.D. (0.05)
Number of plants (N)	67	62	21	81	76	—	—
Frequency of nodulated plants (%)	45	44	24	32	97	53	—
Air temperature (C)	22.4	22.5	20.9	18.8	13.6	17.8	3.0
Soil temperature (C)	17.7	13.8	15.1	17.5	10.7	13.8	2.3
Soil moisture 0–20 cm (g/kg)	70	63	47	76	105	87	24
Soil moisture 20–40 cm (g/kg)	74	70	93	84	125	101	26
Leaf water potential (−MPa)							
Nodulated plants	8.3	10.4	11.2	12.2	9.1	9.7	1.8
Nonnodulated plants	8.2	9.8	16.8	13.1	8.7	11.4	2.0
Shoot weight (g)							
Nodulated plants	17.0	25.7	4.5	9.8	9.5	13.5	12.5
Nonnodulated plants	15.0	50.7	41.8	16.8	12.9	27.2	20.4
Root weight (g)							
Nodulated plants	57.2	45.4	4.7	14.3	6.5	23.6	41.6
Nonnodulated plants	22.3	64.2	65.4	26.4	12.6	38.6	28.5
Nodule weight (g/plant)	0.04	1.21	0.10	0.10	0.43	0.42	N.S.
Day of year	157	167	170	213	230	202	18.7
Hour	11.1	13.3	11.2	13.6	11.4	12.0	0.6
$N_2[C_2H_2]$ activity (µ moles/h)	8.4	4.4	6.6	2.7	11.4	8.2	4.3

Difference between means required for statistical significance ($P < .05$).
NS – not significant.

with air and soil temperatures, leaf water potential, day of year, and root weight, but negatively related to the other variables.

Plants for which nodules could not be found weighed more than those with nodules. Average shoot weight of the 145 plants without nodules was 27.2 g in contrast to 13.5 g for the 162 nodulated plants. This was probably a function of plant age. Young, actively growing plants of *L. argenteus* were better nodulated than more mature plants. Nodulated plants averaged 45, 44, 24, 32, and 97% at the five sites along the gradient, with the highest elevation having the greatest proportion of plants with nodules. Differences in shoot weight of nonnodulated and nodulated plants at the highest and lowest elevations were not statistically significant ($P > .05$), whereas differences between the means for the three intermediate elevation sites were significant ($P < .05$). Nodules of *L. argenteus* are perennial, and nodule number was assumed to be relatively stable throughout the duration of the study.

Differences in root biomass also were noted, but these could have been caused by incomplete excavation of the root systems of plants for which nodules were easily found. Pegtel (1980) observed that all root systems of *L. laxiflorus*, *L. lepidus*, and *L. polyphyllus* had functioning nodules. Although roots were excavated to as deep as 100 cm in the present study and the roots carefully examined, nodules might have been overlooked or the excavation might not have been deep or extensive enough to expose all nodules. Rocky soil impeded the digging of some plants, especially at the 2454-m study area. Holter (1978) was of the opinion that determination of root biomass and number of nodules was impractical in the field. He believed that acetylene reduction rates related to these quantities would not be useful and that rates should be expressed on a per plant, per shoot, or per gram of aboveground biomass basis.

Dinitrogen fixation rates of other native perennial lupine species were lower for older plants and plants growing on droughty sites than for younger plants and plants growing on more favorable sites (McNabb and Geist 1979). Acetylene reduction activity for *L. argenteus* on Francis Peak was much greater for plants at the 2713-m elevation than at the four lower sites. The rate of 11.4 µ moles of

TABLE 2. Simple correlations (r) of environmental and physiological variables with acetylene reduction rates, $N_2[C_2H_2]$, of nodulated *Lupinus argenteus* plants. Rates are expressed as μ moles of ethylene/h/g nodule fresh weight.

Correlated variable	Study sites		
	All	Early group	Late group
Elevation (m)	0.06	0.15	−0.15
Air temperature (C)	−0.04	−0.08	0.49**
Soil temperature (C)	−0.10	−0.15	0.36**
Soil moisture 0–20 cm (g/kg)	0.16*	0.21*	−0.31*
Soil moisture 20–40 cm (g/kg)	0.20*	0.20*	−0.28*
Leaf water potential (−MPa)	−0.18*	−0.14	0.08
Shoot weight (g)	0.05	0.03	0.30*
Root weight (g)	−0.03	−0.01	−0.04
Nodule weight (g)	0.10	−0.04	0.38**
Day	0.00	−0.18	−0.13
Hour	−0.28**	−0.01	−0.04

$^*P < .05$.
$^{**}P < .01$.

TABLE 3. Rank of importance of independent variables, standardized multiple regression coefficients (Beta), and multiple correlation coefficients (R) from the stepwise multiple regression analysis of acetylene reduction rates, $N_2[C_2H_2]$, of nodulated *Lupinus argenteus* plants. Rates are expressed as μ moles of ethylene/h/g nodule fresh weight.

Independent variable	Study area grouping					
	All		Early		Late	
	Rank	Beta	Rank	Beta	Rank	Beta
Elevation (m)	6	0.12	5	0.30	7	−0.22
Air temperature (C)	7	0.15	9	0.13	1	0.28
Soil temperature (C)	11	0.01	3	−0.25	6	0.55
Soil moisture 0–20 cm (g/kg)	8	−0.08	1	0.15	10	−0.09
Soil moisture 20–40 cm (g/kg)	2	0.23	10	−0.08	8	0.29
Leaf water potential (−MPa)	5	−0.17	11	−0.02	5	−0.30
Shoot weight (g)	4	0.09	7	0.10	3	0.27
Root weight (g)	10	0.01	8	0.05	4	−0.36
Nodule weight (g)	3	0.13	4	−0.10	2	0.41
Day	9	0.06	6	−0.20	11	−0.01
Hour	1	−0.22	2	−0.18	9	−0.10
R	.38		.36		.74	

ethylene per hour per g of fresh nodule weight at the 2713-m elevation was 52% greater than the average rate of the 88 plants from the lower elevations.

Simple correlations (Table 2) indicated that soil moisture, leaf water potential, and hour of sampling were significantly ($P < .05$) associated with reduction activity. An examination of the means in Table 1 led to grouping of the study areas into two categories according to mean time of sampling. Nodules from the 2027- and 2454-m elevations were collected later in the afternoon than those from the 1478-, 2256-, and 2713-m areas. The early group mean sampling time and standard error were 11.3 ± 0.01 hours, but those of the late group were 13.4 ± 0.01 hours, or more than 2 hours later in the day. Soil moisture was the only factor correlated with activity of nodules from plants in the early group. Air and soil temperatures, shoot and root weights, as well as soil moisture, were correlated with activity of nodules from plants in the late group. *Trifolium pratense* L. and *Medicago lupulina* L. fixed very little nitrogen when soil moisture was reduced to 8% or less (Holter 1978). Table 1 shows that soil moisture averaged less than that in the surface to 40 cm depths at the four lower study areas on Francis Peak.

Causal relationships among the variables were examined by forward stepwise multiple regression. When all available data were considered, hour of day at which the plants were sampled and soil moisture below 20 cm were the two most influential independent variables determining acetylene reduction rates (Table 3). They jointly generated a multiple correlation coefficient, R, of .27 and explained 7% of the variation in per plant nitrogen fixation activity, $N_2[C_2H_2]$. Peak activity occurred from 11:00 a.m. to 12:00 noon when the rate averaged 12.0 μ moles of ethylene per hour per g nodule fresh weight. Samples taken the preceding hour produced a reduction rate of only 7.2 μ moles. Mean rates then dropped to 8.4, 5.0, 3.1, 2.6, and 3.5 μ moles for subsequent one-hour intervals in the afternoon.

Hour of sampling and leaf water potential were positively and significantly ($P < .05$) associated, $r = .47$. The impact of hour on acetylene reduction activity probably was due to increased drought stress as the day progressed. This seemed to be particularly true at the 2713-m elevation, which was sampled at four times. One plant sampled at 10:00 a.m. had a leaf water potential of −0.96 MPa, whereas 47 plants sampled at 11:00 a.m. averaged −0.78 MPa. Drought stress then increased markedly, as the 19 plants sampled at 12:00 p.m. had an average leaf water potential of −1.13 MPa. The stress increased still further for the 7 plants sampled at 1:00 p.m., which averaged −1.24 MPa.

Air temperature changed from a low of 15.4 C at 11:00 a.m. to a high of 26.7 C at 4:00 p.m. Air temperature was positively correlated with acetylene reduction activity and was the single most important independent variable when data from the late grouping of study areas were considered (Table 2). Nodule weight was the second most influential variable for the late group and also was important for the early group (Table 3). This was true even though the activity was expressed on a gram nodule fresh weight basis. The degree of hydration of nodules apparently played a role in the nitrogen fixation rates of these plants.

The other independent variables were of lesser value in predicting nitrogen fixation activity. Shoot and root biomass were strongly related to acetylene reduction in four legume species studied by Holter (1978). These were of lesser importance in this study of *L. argenteus*. However, variation in the 11 independent parameters measured and listed in Table 3 explained only 14% of the observed variation in activity. The remaining 86% of the variation in fixation was caused by factors not accounted for in this study, but which must have been, in some way, related to the time of sampling. Separation of the study areas into two groups on the basis of mean sampling time resulted in much stronger predictive relationships for the late group. The multiple correlation coefficient was $R = .74$ (Table 3), and the predictive function explained more than half the observed variation in acetylene reduction rates. For plants in the early group, factors other than those measured in this study profoundly influenced the dinitrogen fixation rates of *L. argenteus* plants on the slopes of Francis Peak. Although acetylene reduction rates of *L. argenteus* could not be accurately predicted from the variables evaluated in this study, plants of *L. argenteus* were nodulated and capable of reducing acetylene along an elevational gradient on Francis Peak.

Acknowledgments

This work was supported by U.S. Department of Agriculture Grant 5901-0410-9-0277-0 and the U.S. Department of Agriculture, Agricultural Research Service, and the Department of Range Science, Utah State University, Logan, Utah, under Cooperative Agreement No. 58-9AHZ-0-477. We gratefully acknowledge the capable technical assistance of Dennis Rinehart and Michael Huffman.

Literature Cited

Farmer, E. E., and J. E. Fletcher. 1971. Precipitation characteristics of summer storms at high-elevation stations in Utah. USDA Forest Service Research Paper INT-110. 24 pp.

Farnsworth, R. B., E. M. Romney, and A. Wallace. 1978. Nitrogen fixation by microfloral-higher plant associations in arid to semiarid environments. Pages 17–19 *in* N. E. West and J. J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchinson, and Ross, Inc., Stroudsburg, Pennsylvania.

Holter, V. 1978. Nitrogen fixation of 4 legumes in relation to aboveground biomass, root biomass, nodule number and water content of the soil. Oikos 31: 230–235.

Johnson, D. A., and M. D. Rumbaugh. 1981. Nodulation and acetylene reduction by certain rangeland legume species under field conditions. Journal of Range Management 34: 178–181.

______. 1986. Field nodulation and acetylene reduction activity of high-altitude legumes in the western United States. Arctic and Alpine Research 18: 171–179.

Johnston, R. S., and R. D. Doty. 1972. Description and hydrologic analysis of two small watersheds in Utah's Wasatch Mountains. USDA Forest Service Research Paper INT-127. 53 pp.

McNABB, D. H., AND J. M. GEIST. 1979. Nitrogen fixation potential of native lupines in western conifer ecosystems. Page 217 *in* Agronomy abstracts. American Society of Agronomy, Madison, Wisconsin.

PEGTEL, D. M. 1980. Evidence for ecotypic differentiation in *Lupinus*-associated *Rhizobium*. Acta Botanica Neelandica 29: 429–441.

PHILLIPS, L. L. 1955. Revision of the perennial species of *Lupinus* in North America. Washington State College Research Studies 23: 161–201.

SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, AND E. A. HEMMINGSEN. 1965. Sap pressure in vascular plants. Science 148: 339–346.

WALSH, J. F., D. F. BEZDICEK, A. M. DAVIS, AND D. L. HOFFMAN. 1983. Nitrogen fixation capabilities of plant introduction accessions of pasture and range forage legumes. Agronomy Journal 75: 474–478.

WAUGHMAN, G. J. 1971. Field use of acetylene reduction assay for nitrogen fixation. Oikos 22: 111–113.

WESTERMANN, D. T., AND J. J. KOLAR. 1978. Symbiotic $N_2[C_2H_2]$ fixation by bean. Crop Science 18: 986–990.

Received 4 December 1990
Revised 8 March 1991
Accepted 27 March 1991

GREAT BASIN NATURALIST
MEMOIRS SERIES

The *Great Basin Naturalist Memoirs* series was established in 1976 for scholarly works in biological natural history of greater length than can be accommodated in the *Great Basin Naturalist*. The *Memoirs* series appears irregularly. Approval for the production is the responsibility of the *Great Basin Naturalist* Editorial Board. Information concerning the production of the *Memoirs* series can be obtained from James R. Barnes, Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, UT 84602.

GREAT BASIN NATURALIST MEMOIRS

All *Memoirs* are available for purchase. Direct inquiries to: Editorial Office, 290 MLBM, Brigham Young University, Provo, UT 84602. Only U.S. currency or checks or money orders drawn on U.S. banks are accepted. These should be made out to *Great Basin Naturalist*. Please include $3 per copy for mailing and handling charges except for Nos. 6 and 11. The charge for these volumes is $5 per copy.

No. 1 The birds of Utah. $15
No. 2 Intermountain biogeography: a symposium. $20
No. 3 The endangered species: a symposium. $15
No. 4 Soil-plant-animal relationships bearing on revegetation and land reclamation in Nevada deserts. $15
No. 5 Utah Lake monograph. $15
No. 6 The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. $60
No. 7 Biology of desert rodents. $15
No. 8 The black-footed ferret. $20
No. 9 A Utah flora. $40
No. 10 A reclassification of the genera of Scolytidae (Coleoptera). $20
No. 11 A catalog of Scolytidae and Platypodidae (Coleoptera), part 1: bibliography. $50
No. 12 Research in the Auchenorrhyncha, Homoptera: a tribute to Paul W. Oman. $30

GUIDELINES
FOR MANUSCRIPTS
SUBMITTED TO

THE
GREAT BASIN
NATURALIST

JUNE 1991

BRIGHAM YOUNG UNIVERSITY

Great Basin Naturalist 51(2), 1991, pp. 200–204

GUIDELINES FOR MANUSCRIPTS SUBMITTED TO THE GREAT BASIN NATURALIST

June 1991

The following information is presented to provide authors with guidelines and examples to use in preparing manuscripts submitted to the *Great Basin Naturalist.* Although this is not a comprehensive treatise, we believe the guidelines address some of the most common problems encountered by our authors. We recommend the *CBE Style Manual*, 5th edition (Council of Biology Editors, Suite 1200, 230 N. Michigan Avenue, Chicago, IL 60601-5961 USA; $24), for more in-depth discussions.

Manuscript Preparation

Type manuscripts on standard bond (22 × 28 cm), leaving 2.5-cm margins on all sides, and submit three copies to the *Great Basin Naturalist*. Please do not send diskettes. Manuscripts printed on a dot-matrix printer should be near-letter or letter quality. To allow reviewers and editors sufficient space for notations, we require double-spacing throughout the manuscript—title page, abstract, text, literature cited, appendices, tables, and figure legends. Either 12-pitch (elite) or 10-pitch (pica) type is acceptable (10-pitch is preferred); right-margin justification is also acceptable. However, if right justification is used, avoid hyphenating words at the ends of lines. This includes both hyphenated words and words divided between syllables. (Hyphenation should be turned off on word-processing equipment.) Number all pages consecutively but omit the number on the title page.

Manuscripts may be submitted as either scientific papers or notes, the major difference being the lack of an abstract in notes (see section under Abstract). In addition, notes are generally shorter communications.

Title page. Included on the title page are the title, names and addresses of authors, a running head, and footnotes to indicate change of address. Also, indicate the author to whom correspondence should be addressed if other than the first author.

- The *title* should be specific and concise (no longer than 15 words). It identifies the article's content or main topic rather than its conclusions. If appropriate, it should include the name of the organism(s) involved. The use of order and family names for species that may be unfamiliar to many readers is appropriate.

- To avoid confusion, we recommend using *full names of authors* rather than initials. Omit academic degrees and professional positions, but cite the department and institution in which the research was done, also the *mailing address* and postal code. If the present address differs from the research institution, include the updated address for correspondence and reprint requests.

- Please provide a *running head* of fewer than 40 letters and spaces. This is a shorter, but nevertheless descriptive, version of the title; it will appear at the top of each right-hand page of the published article.

Abstract. The abstract aids the reader in comprehending the essence of the author's research. It should state the objectives and purpose of the study, methods and/or materials used, results, and conclusions of the research. If appropriate, scientific and common names of organisms should be included, with special emphasis on new taxa or distribution records. Limit the abstract to approximately 250 words.

- Following the abstract are 6–12 *key words*, listed in order of decreasing importance, to be used for indexing. These words should reflect the central topics of the article and may be from the title, abstract, or text. Please list key words for both notes and articles.

Text. The significance of the text, or, more specifically, the author's prose style, cannot be underestimated. Ultimately, a scientific article must capture the attention of its readers by the importance of its content and its clarity of expression. Chapter 5, Prose Style for Scientific Writing, in the *CBE Style Manual* offers helpful suggestions for achieving succinctness and clarity, and avoiding verbiage and distressing grammatical errors.

Although frequently avoided, particularly in scientific articles, the active voice is the one in which people usually speak and write. It is perfectly acceptable and very useful in scientific writing. Not only is active voice ("We determined") less wordy and ambiguous than passive voice ("It was determined"), but its use is also less likely to result in dangling participles and other misplaced modifiers. When appropriate, use active voice.

Verb tense is another area that deserves comment. Completed procedures and observations are described in the past tense ("was," "were"), but present tense is used when presenting directions, conclusions, generalizations, and references to stable or current conditions.

Because *Great Basin Naturalist* articles cover diverse disciplines, we ask our authors to avoid excessive use of unfamiliar abbreviations, jargon, and overly technical vocabulary. Such terms hinder understanding by members of other disciplines and prevent a free exchange of ideas.

For maximum clarity, the body of the text should be divided into the following sections.

- *Introduction.* The introduction need not be long, but it must adequately introduce the research. At the end of the introduction, clearly state the purpose of the research.

- *Methods.* The methods section should contain all the information necessary for other researchers to duplicate the study. The description of the experimental or sampling design should be clear to the reader. Use a simple figure to present this information if it helps the reader understand the procedures. Another vital part of this section is a description of all statistical procedures used.

- *Study Site Description.* It may be appropriate to include a description of the study area in a separate section. This usually precedes the methods section, but it may also be contained within that section.

- *Results.* The results should be separate from the discussion. In this section, state the results using text, figures, tables, or any workable combination thereof. This section is not for the interpretation of results.

- *Discussion.* The discussion is the forum in which the study results are interpreted and compared with results from other studies. Interpretations should be consistent with results, and they should correspond with the stated purpose(s) of the research.

We highly recommend the following article as one that is helpful to authors in writing and critiquing their own work:

Kuyper, B. J. 1991. Bringing up scientists in the art of critiquing research. BioScience 41:248–150.

Easily understood, effectively placed headings and subheadings help the reader quickly grasp the content and structure of the paper. The *Great Basin Naturalist* uses three levels of headings within textual material.

- *Primary headings* are centered in all capital letters with space above and below. In general, primary headings should be restricted to STUDY AREA, MATERIALS AND METHODS, RESULTS, DISCUSSION, CONCLUSIONS, ACKNOWLEDGMENTS, LITERATURE CITED, and APPENDIX, or variations of any of the above. Do not use INTRODUCTION as a heading.

- *Secondary headings* are centered in upper- and lowercase letters with space above and below.

- *Tertiary headings*, set in all capitals, are indented from the left margin and followed by a period and a 1-em dash (two hyphens in typescript). Do not use secondary or tertiary headings unless major sections are long and/or the text is complex. In articles requiring only two levels of organization, tertiary headings should be used directly under primary headings.

Literature Cited. References to published literature and unpublished documents used in an article are cited in both the text and a separate bibliographic section.

References in the text are cited by author and date: e.g., Potter (1980) or (Potter 1980). Multiple citations should be separated by commas and listed in chronological order (Baker 1968, Flake 1973, Agnew 1986). In citations having more than two authors, use "et al." after the name of the first author (MacCracken et al. 1985).

Use the heading LITERATURE CITED for the list of references following the text. Include only references actually cited in the text. No reference should be included unless the pertinent publication facts have been verified against the original document. Page numbers seem to be particularly susceptible to transposition and other typographical errors. The responsibility for accuracy of reference material lies with the author, not the copy editor.

The list of literature cited must be alphabetical by authors' surnames. Initials are usually sufficient for given names unless confusion would result when family names and initials are identical for different authors. In such cases write out the first given name for each author.

The *Great Basin Naturalist* no longer abbreviates titles of periodicals and names of publishers. Include full titles as they appear on the title page, but omit initial articles. *The American Midland Naturalist* and *The Great Basin Naturalist* become, respectively, *American Midland Naturalist* and *Great Basin Naturalist.*

As a general rule, too much bibliographical information is better than too little. Unnecessary data can be deleted.

Following are examples of the most common types of bibliographic references.

- *Journals*

Arcos, M. L., A. de Vicente, M. A. Morinigo, P. Romero, and J. J. Borrego. 1988. Evaluation of several selective media for recovery of *Aeromonas hydrophila* from polluted waters. Applied and Environmental Microbiology 54: 2786–2792. [Only the initials of the first author are inverted; use the first author's name and "et al." for papers with seven or more authors.]

Ferguson, J. H., and C. H. Lowe. 1969. Evolutionary relationships in the *Bufo punctatus* group. American Midland Naturalist 81: 435–466. [Issue numbers are not included unless the journal is numbered by issue rather than by volume; the issue, supplement, or part number is then included in parentheses after the volume number:

3(6):42–57 56(suppl. 4):8–13
2(3, pt. 4):2–5.]

Tove, M. H., and D. L. Fischer. 1991. [If the year of publication has not been determined, use "In press" in place of the date.] Recent changes in the status of wintering gull populations in Utah. American Birds. [Omit volume and pagination for in-press citations.]

- *Books*

Brady, N. C. 1974. The nature and properties of soils. 8th ed. Macmillan Publishing Co., Inc., New York. 639 pp.

Snedecor, G. W., and W. G. Cochran. 1971. Statistical methods. Iowa State University Press, Ames. [Repeating the state name would be redundant.]

- *Parts of books*

Smith, H. D., and C. D. Jorgensen. 1975. Reproductive biology of North American desert rodents. Pages 305–330 *in* I. Prakash and P. K. Ghosh, eds., Rodents in desert environments. Dr. W. Junk Publishers, The Hague, Netherlands.

- *Proceedings*

Schenbeck, G. L. 1982. Management of black-tailed prairie dogs on the National Grasslands. Pages 207–217 *in* R. M. Timm and R. J. Johnson, eds., Proceedings of the Fifth Great Plains Wildlife Damage Control Workshop. University of Nebraska, Lincoln.

- *Theses/Dissertations*

Cramer, K. L. 1988. Reproduction and life history patterns of *Peromyscus maniculatus* and *Perognathus* spp. in the northern Bonneville Basin, Utah. Unpublished dissertation, Utah State University, Logan. 101 pp.

- *Miscellaneous*

Tueller, P. T., C. D. Beeson, R. J. Tausch, N. E. West, and K. H. Rea. 1979. Pinyon-juniper woodlands of the Great Basin: distribution, flora, and vegetal cover. USDA Forest Service Research Paper INT-229. Intermountain Forest and Range Experiment Station, Ogden, Utah. 22 pp. [Subtitles are lowercased.]

Literature citations of reports will not be used unless adequate information has been provided for the reader to readily locate the reference.

Appendices. Long lists or material related only indirectly to the topic should be included in an appendix. Lists of specimens examined, for example, would be appropriate.

Tables. Tables are costly to typeset and therefore should be used only when they are deemed the most effective means of presenting and summarizing data. If the data can be described in one or two sentences within the text, do not present the information in a table. Tables should be self-explanatory. The title, headings, and footnotes must contain sufficient information for the reader to understand the table without referring to the text. This will be achieved if the format is clear, simple, and well organized. Also, tables of similar information presented in similar or parallel formats will aid the reader. Chapter 6 of the *CBE Style Manual* offers helpful suggestions on compiling, presenting, and condensing information in tabular formats.

All tables should be numbered sequentially. Each table must be typed on a separate sheet(s), given a complete, intelligible title, and referred to by number in the text. The title describes the topic or general trends shown in the table; it should also include species, localities, and dates of study when appropriate. Include the number of samples (for example, $N = 24$) in the title or in a column heading, whichever would be more beneficial to the reader.

Make headings within tables brief and grammatically consistent with each other. Capitalize only the first word of column heads and items in stubs (row headings); do not use all uppercase letters. Footnotes to tables should be kept to a minimum. Asterisks (*), one, two, or three, should be used for probability, $P < .05$, .01, and .001, respectively. Lowercase letters are used to denote other footnotes.

Finally, a table that fits into one column of the *Great Basin Naturalist* two-column format is more likely to be printed close to its corresponding text. This, of course, is a relatively simple method of enhancing reader understanding.

Figures. Well-designed and prepared illustrative materials, whether photographs or black-and-white artwork, not only augment and clarify written material but also provide visual enhancement. On the other hand, poorly prepared graphics may minimize the author's or the journal's credibility.

In considering the addition of illustrations to an article, be certain the text is long enough to accommodate the artwork. In most cases two pages of typescript are required for each figure or table; three pages are preferred. When submitting an article for review, please do not send original photographs or black-and-white artwork. High-quality photocopies are adequate.

- *Photographs* (generally referred to as halftones), because of the nature of the reproduction process, are approximately two to three times as expensive to produce as line copy (black-and-white artwork). We recommend keeping halftones to a minimum. When they are included, please submit glossy originals with sharp focus, a full range of tonal values, and suitable contrast. Photographs that are slightly gray (low contrast) reproduce better than those with high contrast.

Photographs submitted with the final manuscript upon acceptance by the *Great Basin Naturalist* should be no larger than 22 x 28 cm. Ideally, the printed size will be between 50% and 100% of the original size. Smaller reductions tend to darken and lose details. Photographs can also be enlarged up to about 150% of original size without adversely affecting quality. Photomicrographs and electron micrographs should include a scale on the photograph or on an overlay.

- *Line copy* is black-and-white artwork. Prepared on a white background with black lines, it contains no grays. Graphs, diagrams, and charts fall into this category. Technical pens, flexible pens, and brushes, all used with black India ink, can produce line drawings, depending on the type of illustration desired. Technical pens will give evenly weighted lines suitable for graphs and charts. Flexible pens and brushes give smooth, tapered lines or softer, fuzzy effects, respectively.

Although line copy does not contain grays, the effect of gray areas can be achieved by using stippling, cross-hatching, or line contouring. Patterned screens with adhesive backings are also frequently used.

Line drawings should not be enlarged for publication, as enlargement reveals—and magnifies—flaws that may not be obvious on the original. Reductions of black-and-white artwork should not exceed 50%. It is important that all lines, symbols, and letters be large enough on the original to withstand reduction and still maintain integrity and/or legibility.

- *Computer-generated graphics*, increasingly available in many institutions, are acceptable forms of black-and-white artwork as long as they are produced on laser, rather than dot-matrix, printers. The same requirements that apply to line art also apply to computer graphics.

- *General considerations for illustrations:*

1. For the sake of consistency, multiple pieces of artwork for one article or a series of articles should be prepared, if possible, by the same artist. A uniform reduction of multiple pieces will also aid consistency.

2. The general ratio of 2:3, in either a vertical or horizontal orientation, will result in artwork compatible with the *Great Basin Naturalist's* page and/or column dimensions.

3. Place necessary identifications, i.e., symbols, regression formulas, and scale bars, directly on the figure rather than in the figure legend.

4. Use symbols for data points, particularly on graphs. The most common are ○, ●, △, ▲, □, ■, ◇, ◆.

5. Identify all artwork on the back. Using a soft blue pencil, mark author and figure number, and indicate "top."

General Style and Usage Conventions

Provide the scientific name (genus and species) of all organisms when first mentioned in the vernacular form in both abstract and text even if the name appears in the title.

Use a comma to separate the elements (words, phrases, or clauses) of a simple series of more than two. A comma precedes the "and" or "or" (e.g., blue grama, buffalograss, and needleleaf sedge).

Underline generic and specific names in text (they will be italicized in print). Do not use italics or boldface type in manuscripts.

Follow *Webster's Ninth New Collegiate Dictionary* for spelling and word-usage questions. Also, consult *Webster's Third New International Dictionary, Unabridged.*

In numbers consisting of two to four digits, run the numerals together: 1000, 3959. Use comma separators for numbers of five or more digits: 45,808. Use numerals to express any number immediately preceding an abbreviation for a standard unit of measure or expression of time: 5 g, 20 mm, 4 h. In most other situations, use words for numbers one through nine and numerals for larger numbers. However, in a series containing some numbers of 10 or more and some less than 10, use numerals for all.

Write dates with no punctuation: 16 August 1989.

Standard abbreviations are acceptable for units of measure, directions and coordinates, Latin terms (most of which no longer require italics), and statistical terms. Acronyms and other less common abbreviations should be defined when first mentioned by writing out the term and enclosing the abbreviation in parentheses following it.

Always check the most recent issue of the journal for any changes in style or format.

A Final Word

Although we agree that adhering to established rules and maintaining a consistent style are hallmarks of good journalism, we also agree with a statement made in the preface to the University of Chicago's first (1906) edition of a *Manual of Style:*

> Throughout this book it is assumed that no regulation contained therein is absolutely inviolable. . . . Each case . . . must largely be decided upon its own merits. Generally it may be stated that, where no question of good taste or good logic is involved, deference should be shown to the expressed wishes of the author.

Acknowledgments

Portions of this manuscript were extracted from the *CBE Style Manual* (5th ed.), *The Chicago Manual of Style* (13th ed.), *Guidelines for Manuscripts for Publications of the American Society of Mammalogists*, and previously unpublished *Great Basin Naturalist* style guidelines and instructions to authors.

INFORMATION FOR AUTHORS

The *Great Basin Naturalist* welcomes previously unpublished manuscripts pertaining to the biological natural history of western North America. Preference will be given to concise manuscripts of up to 12,000 words.

SUBMIT MANUSCRIPTS to James R. Barnes, Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, Utah 84602. A cover letter accompanying the manuscript must include phone number(s) of the author submitting the manuscript; it must also provide information describing the extent to which data, text, or illustrations have been used in other papers or books that are published, in press, submitted, or soon to be submitted elsewhere. Authors should adhere to the following guidelines; manuscripts not so prepared may be returned for revision.

MANUSCRIPT PREPARATION. Consult Vol. 51, No. 2 of this journal for specific instructions on style and format. These instructions, GUIDELINES FOR MANUSCRIPTS SUBMITTED TO THE GREAT BASIN NATURALIST, supply greater detail than those presented here in condensed form. The guidelines are printed at the back of the issue; additional copies are available from the editor upon request. Also, check the most recent issue of the *Great Basin Naturalist* for changes and refer to the *CBE Style Manual*, 5th edition (Council of Biology Editors, Suite 1200, 230 N. Michigan Avenue, Chicago, IL 60601-5961 USA; $24).

TYPE AND DOUBLE SPACE all materials, including literature cited, table headings, and figure legends. Avoid hyphenated words at right-hand margins. Underline words to be printed in italics. Use standard bond (22 × 28 cm), leaving 2.5-cm margins on all sides.

SUBMIT 3 COPIES of the manuscript. Number all pages and assemble each copy separately: title page, abstract and key words, text, acknowledgments, literature cited, appendices, tables, figure legends, figures.

TITLE PAGE includes an informative title no longer than 15 words, names and addresses of authors, a running head of fewer than 40 letters and spaces, footnotes to indicate change of address and author to whom correspondence should be addressed if other than the first author.

ABSTRACT states the purpose, methods, results, and conclusions of the research. It is followed by 6–12 key words, listed in order of decreasing importance, to be used for indexing.

TEXT has centered main headings printed in all capital letters; second-level headings are centered in upper- and lowercase letters; third-level headings begin paragraphs.

VOUCHER SPECIMENS. Authors are encouraged to designate, properly prepare, label, and deposit high-quality voucher specimens and cultures documenting their research in an established permanent collection, and to cite the repository in publication.

REFERENCES IN THE TEXT are cited by author and date: e.g., Martin (1989) or (Martin 1989). Multiple citations should be separated by commas and listed in chronological order. Use " et al." after name of first author for citations having more than two authors.

ACKNOWLEDGMENTS, under a centered main heading, include special publication numbers when appropriate.

LITERATURE CITED, also under a centered main heading, lists references alphabetically in the following formats:

Mack, G. D., and L. D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. Journal of Wildlife Management 44: 695–700.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Coulson, R. N., and J. A. Witter. 1984, Forest entomology: ecology and management. John Wiley and Sons, Inc., New York. 669 pp.

TABLES are double spaced on separate sheets and designed to fit the width of either a single column or a page. Use lowercase letters to indicate footnotes.

PHOTOCOPIES OF FIGURES are submitted initially with the manuscript; editors may suggest changes. Lettering on figures should be large enough to withstand reduction to one- or two-column width. Originals must be no larger than 22 × 28 cm.

NOTES. If your manuscript would be more appropriate as a short communication or note, follow the above instructions but do not include an abstract.

A CHARGE of $45 per page is made for articles published; the rate for subscribers will be $40 per page. However, manuscripts with complex tables and/or numerous half-tones will be assessed an additional charge. Reprints may be purchased at the time of publication (an order form is sent with the proofs).

FINAL CHECK:

- Cover letter explains any duplication of information and provides phone number(s)
- 3 copies of the manuscript
- Conformity with instructions
- Photocopies of illustrations

(ISSN 0017-3614)

GREAT BASIN NATURALIST Vol. 51, No. 2, June 1991

CONTENTS

Articles

Evolutionary differentiation within the northern Great Basin pocket gopher, *Thomomys townsendii*. I. Morphological variation .... Mary Anne Rogers 109

Evolutionary differentiation within the northern Great Basin pocket gopher, *Thomomys townsendii*. II. Genetic variation and biogeographic considerations .... Mary Anne Rogers 127

Ecological relationships of curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) communities in Utah and implications for management. .... James N. Davis and Jack D. Brotherson 153

Site characteristics and habitat requirements of the endangered dwarf bearclaw poppy (*Arctomecon humilis* Coville, Papaveraceae) .... Deanna R. Nelson and Kimball T. Harper 167

Bromus invasions on the Nevada Test Site: present status of *B. rubens* and *B. tectorum* with notes on their relationship to disturbance and altitude .... Richard Hunter 176

Size, age, and density relationships to curlleaf mahogany (*Cercocarpus ledifolius*) populations in western and central Nevada: competitive implications .... Brad W. Schultz, R. J. Tausch, and Paul T. Tueller 183

Field acetylene reduction rates of *Lupinus argenteus* along an elevational gradient .... M. D. Rumbaugh and D. A. Johnson 192

Guidelines for manuscripts submitted to the *Great Basin Naturalist* 200

10'8
stracted
[illegible]
[illegible]
[illegible])

MCZ
LIBRARY
JUN 0 2 1992
HARVARD
UNIVERSITY

THE GREAT BASIN NATURALIST

VOLUME 51 № 3 — SEPTEMBER 1991

BRIGHAM YOUNG UNIVERSITY

GREAT BASIN NATURALIST

Editor

JAMES R. BARNES

290 MLBM
Brigham Young University
Provo, Utah 84602

Associate Editors

MICHAEL A. BOWERS
Blandy Experimental Farm
University of Virginia
Box 175
Boyce, Virginia 22620

JEANNE C. CHAMBERS
USDA Forest Service Research
860 North 12th East
Logan, Utah 84322-8000

JEFFREY R. JOHANSEN
Department of Biology
John Carroll University
Cleveland, Ohio 44118

PAUL C. MARSH
Center for Environmental Studies
Arizona State University
Tempe, Arizona 85287

BRIAN A. MAURER
Department of Zoology
Brigham Young University
Provo, Utah 84602

JIMMIE R. PARRISH
BIO-WEST, Inc.
1063 West 1400 North
Logan, Utah 84321

Editorial Board. Richard W. Baumann, Chairman, Zoology; H. Duane Smith, Zoology; Clayton M. White, Zoology; Jerran T. Flinders, Botany and Range Science; William Hess, Botany and Range Science. All are at Brigham Young University. Ex Officio Editorial Board members include Clayton S. Huber, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications; James R. Barnes, Editor, *Great Basin Naturalist*.

The *Great Basin Naturalist*, founded in 1939, is published quarterly by Brigham Young University. Unpublished manuscripts that further our biological understanding of the Great Basin and surrounding areas in western North America are accepted for publication.

Subscriptions. Annual subscriptions to the *Great Basin Naturalist* for 1991 are $25 for individual subscribers, $15 for student and emeritus subscriptions, and $40 for institutions (outside the United States, $30, $20, and $45, respectively). The price of single issues is $12. All back issues are in print and available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to the Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, UT 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining the *Great Basin Naturalist* through a continuing exchange of scholarly publications should contact the Exchange Librarian, Harold B. Lee Library, Brigham Young University, Provo, UT 84602.

EDITORIAL PRODUCTION STAFF

JoAnne Abel	Technical Editor
Carolyn Backman	Assistant to the Editor
Heidi Larsen	Production Assistant

Copyright © 1991 by Brigham Young University

Official publication date: 21 October 1991

ISSN 0017-3614
10-91 750 52076

The Great Basin Naturalist

Published at Provo, Utah, by
Brigham Young University

ISSN 0017-3614

Volume 51 30 September 1991 No. 3

Great Basin Naturalist 51(3), 1991, pp. 205–225

A HABITAT EVALUATION PROCEDURE FOR ROCKY MOUNTAIN BIGHORN SHEEP IN THE INTERMOUNTAIN WEST

Tom S. Smith[1], Jerran T. Flinders[1], and David S. Winn[2]

Abstract.—Several habitat evaluation procedures have been developed for bighorn sheep. However, none of these procedures specifically addresses the Rocky Mountain subspecies nor analyzes both the quantity and quality of potential bighorn habitat with regard to minimum viable population (MVP) criteria. This bighorn habitat evaluation procedure combines (1) a quantitative assessment of bighorn range to determine if there are adequate quantities of resources to support an MVP of bighorn sheep, and (2) a qualitative assessment of a range to predict the probable density of bighorns the range can support. Extensive literature review, intensive bighorn research, and a modeling tool, pattern recognition (PATREC), facilitate critical analysis of proposed bighorn reintroduction sites. The resultant stepwise approach to bighorn habitat evaluation enhances the ability of wildlife biologists to make timely and accurate bighorn habitat assessments.

Key words: Habitat evaluation procedure, geographic information system, pattern recognition, minimum viable population, bighorn sheep, Ovis canadensis canadensis.

The precipitous decline of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) after arrival of American settlers has been well documented (Buechner 1960). As early as 1880, some bighorn herds had been extirpated, while others suffered sharp reductions. Even recently, Jahn and Trefethen (1978) warned that without more effective management, an additional loss of 8% of bighorn sheep could be expected over the next 25 years.

The inability to successfully restore bighorn to former ranges in the western United States results in part from habitat deficiencies that hamper herd growth and persistence. For example, Utah's reintroduction program has not succeeded in restoring Rocky Mountain bighorn to former ranges (Smith et al. 1988). Transplanted sheep have failed to increase, and the current statewide total is approximately equal to the number of transplant animals released (Smith et al. 1988). Reasons for this include: (1) inadequate quantities of available range, (2) severe competition with other ungulates, (3) contact with domestic livestock, (4) improper juxtaposition of key habitat components, (5) inadequate quantities of one or more critical seasonal ranges, and (6) excessive human harassment. More rigorous assessments of proposed reintroduction areas would enhance program success. This habitat evaluation procedure (HEP) is an effort to provide wildlife professionals with a better tool for assessing bighorn habitat quality.

Although several bighorn habitat evaluation procedures have been developed (Ferrier and Bradley 1970, Merritt 1974, Golden and Tsukamoto 1980, Grunigen 1980, Hansen

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.
[2] USDA Forest Service, 324-25th Street, Ogden, Utah 84401.

1980, Wilson et al. 1980, Holl 1982, and Armentrout and Brigham 1988), this HEP has been developed because (1) a Rocky Mountain bighorn sheep HEP is nonexistent and (2) none of the above procedures critically examines actual, or proposed, bighorn ranges for the minimum area necessary to support at least a minimum viable population (MVP) of bighorn sheep. An MVP has been defined by Shaffer (1983) as the smallest isolated population having at least a 95% probability of surviving at least 100 years. Though precise MVP estimates for bighorn sheep are not available, Berger (1990) studied 122 bighorn sheep populations in southwestern United States and found that 100% of the bighorn populations with fewer than 50 individuals went extinct within 50 years. Berger also reported that bighorn populations with more than 100 sheep had persisted for 70 or more years. Consequently, he concluded that 50 bighorn sheep did not constitute a minimum viable population and that managers should strive for herds numbering more than 100 (J. Berger, University of Nevada, personal communications). Additionally, Geist (1975) and others (Sands 1976, Van Dyke et al. 1983) have suggested that wildlife managers should maintain herds of at least 125 individuals if the herds are to survive and persist. Based on this information, it is suggested that 125 individuals represent a current "best estimate" MVP (termed MVPE hereafter) for bighorn sheep populations. Because restoration efforts should strive to establish populations with long-term persistence, this bighorn habitat evaluation procedure assesses the ability of a proposed site to support at least 125 bighorn sheep. This requirement can be relaxed if a reintroduction site is situated so that exchange with nearby herds is expected. In the Mojave Desert of southern California and Nevada, Schwartz et al. (1986) report a stable metapopulation of desert bighorns consisting of 23 subpopulations, many of which fall far short of the 125 MVP estimate. However, due to the close proximity of individual herds and the presence of migration corridors, rams regularly travel between them and maintain gene flow, thereby alleviating the genetics problems which insular, nonmigratory populations face. Therefore, if other populations are close and have access to the reintroduced population, the problem of meeting MVPE criteria may be alleviated. Regarding interherd migrations, Schwartz et al. (1986) cite distances that bighorn have been observed traveling between herds in southern California. Extrapolation of these data to more forested regions should be done with discretion.

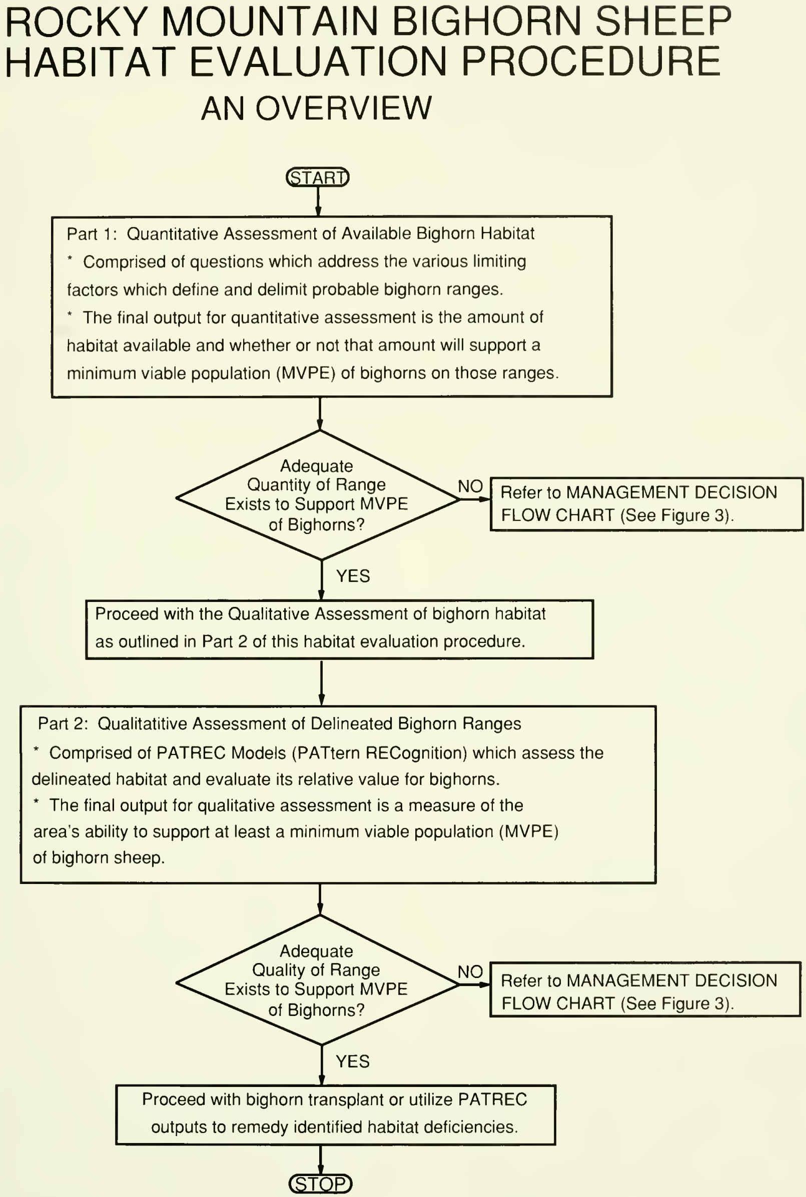
The importance of thorough site evaluation prior to bighorn reintroduction is illustrated by research from Bear Mountain of the Flaming Gorge National Recreation Area in northeastern Utah. Cursorial evaluation of the Bear Mountain transplant area suggests that about 6900 ha of habitat area is available to bighorn sheep. However, when one uses this HEP to identify how much suitable habitat actually exists, only 3800 ha (a 55% reduction) meets the criteria for suitable bighorn habitat (Smith and Flinders 1991). Subsequent research conducted at Bear Mountain verifies the fact that less than half the area is acceptable and usable by bighorn (Smith and Flinders 1991). Hence, even though considered an excellent site by many, Bear Mountain barely meets the minimum space requirements for an MVPE of 125 bighorn sheep.

BIGHORN HEP CAPABILITIES

This bighorn HEP (1) estimates the quantity and quality of occupied, or proposed, bighorn ranges, (2) predicts a site's ability to support at least an MVPE of bighorn sheep, (3) identifies population limiting factors, (4) enables estimation of the effects of management activities on bighorn habitat, (5) assists identification of cost-effective habitat management strategies, and (6) allows use of geographic information systems (GIS) technology for habitat evaluations (Fig. 1). This HEP may be used to evaluate proposed transplant sites or currently occupied ranges.

BIGHORN HEP OVERVIEW

This HEP performs two analyses: estimation of habitat quantity (Part 1) and quality (Part 2). The combination of these two habitat characteristics determines range carrying capacity. Part 1 uses questions regarding bighorn habitat requirements to define probable range area and boundaries. Part 2 employs pattern recognition (PATREC) to assess range quality.



ROCKY MOUNTAIN BIGHORN SHEEP
HABITAT EVALUATION PROCEDURE
AN OVERVIEW

Part 1: Quantitative Assessment of Available Bighorn Habitat

* Comprised of questions which address the various limiting factors which define and delimit probable bighorn ranges.

* The final output for quantitative assessment is the amount of habitat available and whether or not that amount will support a minimum viable population (MVPE) of bighorns on those ranges.

Adequate Quantity of Range Exists to Support MVPE of Bighorns?

Refer to MANAGEMENT DECISION FLOW CHART (See Figure 3).

Proceed with the Qualitative Assessment of bighorn habitat as outlined in Part 2 of this habitat evaluation procedure.

Part 2: Qualitatitive Assessment of Delineated Bighorn Ranges

* Comprised of PATREC Models (PATtern RECognition) which assess the delineated habitat and evaluate its relative value for bighorns.

* The final output for qualitative assessment is a measure of the area's ability to support at least a minimum viable population (MVPE) of bighorn sheep.

Adequate Quality of Range Exists to Support MVPE of Bighorns?

Refer to MANAGEMENT DECISION FLOW CHART (See Figure 3).

Proceed with bighorn transplant or utilize PATREC outputs to remedy identified habitat deficiencies.

Fig. 1. An overview of the Bighorn Habitat Evaluation Procedure.

Bighorn sheep movements are restricted by both intrinsic (behavioral and physical) and extrinsic factors (fences, geographic barriers, etc.). Because bighorn response to habitat variables is reasonably predictable, it is possible to estimate bighorn range size. Although bighorn will occasionally ignore normal barriers to movement, managers should not expect disjunct portions of range, separated by barriers, to contribute significantly to bighorn ranges. A proposed bighorn reintroduction site comprising scattered range segments, crisscrossed with barriers, with key habitat components ineffectively juxtaposed or absent, would ultimately fail to sustain a herd for long. Part 1 presents the normally restrictive barriers and assists in identifying the probable range boundaries, maximum range area, and juxtaposition of key habitat components. Part 1 focuses on critical aspects of bighorn habitat and helps managers determine a site's ability to provide suitable bighorn habitat in the amount needed to support an MVPE of sheep.

Bighorn range quality results from the interaction of many abiotic and biotic characteristics. These interactions create patterns of habitat suitability. The PATREC approach captures in simple mathematical form the process by which most biologists intuitively assess habitat suitability patterns (Grubb 1988). To date, PATREC models have been applied to a variety of wildlife, including Bald Eagles (Grubb 1988), deer (Kling 1980), Sage Grouse (Evans 1983), and bighorn sheep (Holl 1982). For a thorough description of PATREC, see Kling (1980) and Williams et al. (1977). Before proceeding with Part 2 of this HEP, review of PATREC is essential. Particularly helpful is the User's Guide to PATREC for Habitat Evaluation (Kling 1980).

Although most rigorous evaluation of habitat occurs when Parts 1 and 2 are applied, it is not essential that both be used. Part 1 is the key component and cannot be omitted for it defines the ranges that Part 2 analyzes. When insufficient range quantity or irreparable habitat problems have been identified through application of Part 1, site analysis need not proceed. Application of Part 2 requires a more detailed database. It may be used to identify specific weaknesses of a reintroduction site and to determine which remedial approach will yield greatest benefits. We believe that prior to reintroduction of bighorns, rigorous site analysis based on Part 1 alone would greatly enhance the success of many reintroduction efforts.

METHODS

Stepwise discussion of the HEP follows and corresponds to numbered steps in Figure 2.

Part 1

Quantitative Assessment of Available Bighorn Habitat

Sequential questions enable the user to (1) determine the probable range boundaries for an actual, or proposed, bighorn herd, (2) analyze the total area of that range in terms of MVPE criteria, (3) determine if adequate quantities of winter, lambing, and summer ranges exist, and (4) decide if the juxtaposition of habitat components is adequate.

STEP 1.—Any portion of range that might allow contact between bighorns and their exotic relatives, including domestic sheep and goats, should be excluded from consideration.

Recent research has verified the incompatibility of domestic sheep, goats, and bighorn sheep on the same ranges (Foreyt 1990). Exotic relatives of bighorn sheep, including mouflon sheep (*Ovis ammon musimon*), barbary sheep (*Ammotragus lervia*), and ibex (*Capra ibex*), are sources of disease, competition, and genetic pollution for bighorn sheep (Geist 1988). Domestic sheep (and goats in one instance) have been implicated as the disease source responsible for several recent bighorn sheep catastrophic die-offs (Jessup 1981, Goodson 1982, Capurro 1988, Coggins 1988). Bighorn sheep and mouflon sheep readily cross and produce viable offspring. Impure, genetically polluted bighorns have no historic, conservation, or scenic value. Although minimum distances for separation of bighorn and exotics, including domestic sheep, have been suggested (Holl and Bleich 1983, Armentrout and Brigham 1988, Coggins 1988), the potentially catastrophic consequences of exotic-bighorn interactions justify a policy of absolute separation. If separation is not possible, the area should not be considered potential bighorn range until exotics are removed. Ranges recently vacated of exotics require no resting period before bighorn transplanting because the pneumophillic diseases that precipitate die-offs are transmitted by direct contact only.

STEPS 2 AND 3.—Estimate the probable range boundaries of available bighorn habitat.

Steps 2 and 3 determine whether bighorns are already present on the site and, if so, their range boundaries. When the bighorn herd is established and approximate range boundaries known, steps 4–8 can be disregarded, since their role is to estimate the probable extent of bighorn ranges.

STEP 4.—Delineate and buffer core bighorn habitat areas.

All bighorn habitat is dependent upon the presence and extent of escape terrain areas. Escape terrain comprises slopes greater than 60% (about 27°) that have occasional rock outcroppings whereon bighorn can outmaneuver predators and find secure bedding areas. For a more thorough discussion of escape terrain, see Van Dyke et al. (1983). Because escape terrain provides antipredator protection, bedding and lambing areas, and areas of lesser snowpack, it has been identified as the most critical habitat component for bighorns (Buechner 1960, Ferrier and Bradley 1970, Geist 1971, Wilson et al. 1980, Van Dyke et al. 1983). Specialized for leaping and climbing rather than for running on flat terrain (Geist 1971), bighorns are tied to escape terrain and seldom venture far from it (McCann 1956, Oldemeyer et al. 1971, Brown 1974, Van Dyke et al. 1983, Hansen 1984, Gionfriddo and Krausman 1986). On Bear Mountain, 95% of all bighorn activity occurred within 300 m of escape terrain (Smith and Flinders 1991). Therefore, areas not within 300 m of escape terrain should be excluded when evaluating bighorn ranges.

Occasionally, a segment of range is bounded on two or more sides by escape terrain. If the range between escape terrain areas is 1000 m wide or less, the entire area should be included as potential bighorn habitat. In such situations, bighorn are apparently willing to roam farther from safety (up to 500 m) because of the increase in escape route options (Van Dyke et al. 1983).

STEP 5.—Identify additional restrictions for range boundary determinations including natural and man-made barriers to bighorn movement.

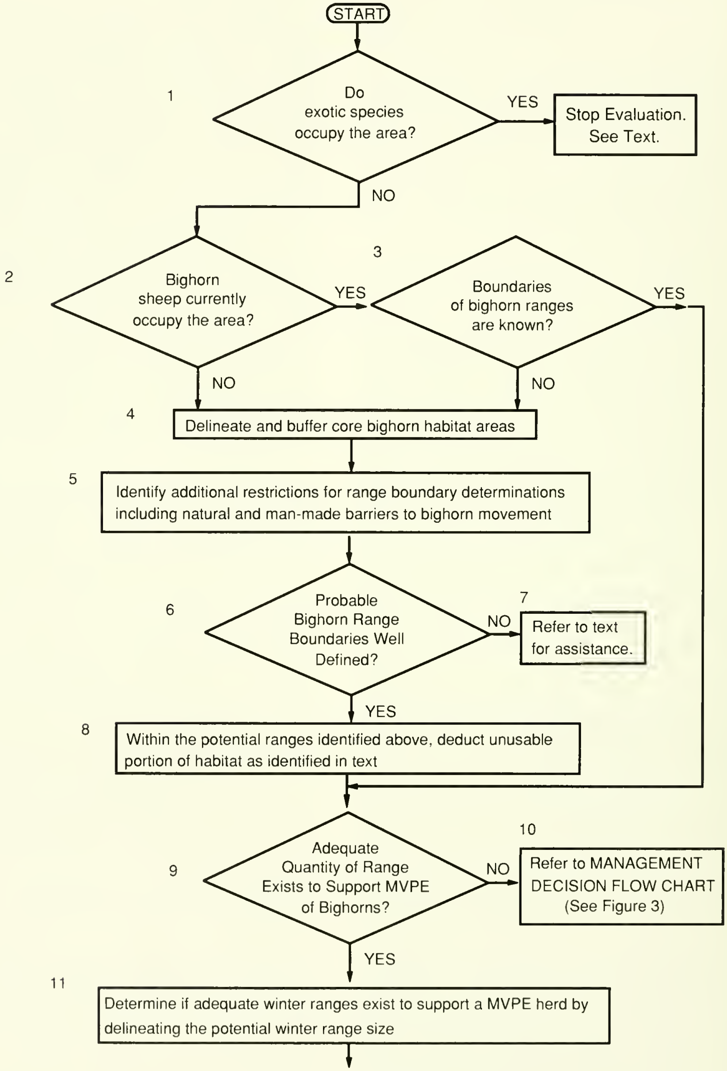
A. Natural barriers

1. *Water: swift and/or wide rivers and lakes.* Although Cowan (1940) occasionally observed bighorn swimming, water has been noted elsewhere to effectively delimit bighorn ranges (Graham 1980, Wilson et al. 1980, Smith and Flinders 1991). Rivers and lakes break range continuity and are commonly barriers to bighorn movements. Consequently, because bighorn herds rarely inhabit both sides of a canyon when a major river is present, managers should consider one side, but not both sides, of a continuous water body as bighorn range.

2. *Dense vegetation.* Smith and Flinders (1991), Brundige and McCabe (1986), Risenhoover and Bailey (1980), Wilson et al. (1980), McCann (1956), Cowan (1940) and others have stated that bighorn sheep hesitate crossing even narrow tracts of dense vegetation, particularly timber. Aversion to low visibility, likely a predator-avoidance strategy, restricts bighorn movements. Dense timber, thick shrubs, and lush herbaceous tracts often form impassable barriers to bighorns. For this reason, low-visibility areas at least 100 m wide should be considered movement barriers to bighorn sheep. Because these areas can restrain bighorn from utilizing more suitable terrain beyond, they need to be identified. Smith and Flinders (1991) present methodology for determining the horizontal visibility of an area. They found that areas with less than 80% horizontal visibility were little used by bighorns, regardless of their other qualities (e.g., distance to cliffs, herbaceous plant production, etc.).

3. *Cliffs: continuous, nontraversable cliff complexes.* Although bighorn rely heavily on cliffs, some cliff complexes do not qualify as escape terrain, but rather function as barriers to movement. Sheer, vertical cliffs, lacking negotiable terrain, can limit bighorn movements and range size. Of particular concern are continuous bands of sheer cliffs because they may isolate other

PART 1: QUANTITATIVE HABITAT ASSESSMENT FLOW DIAGRAM


START
1
Do exotic species occupy the area?
YES
Stop Evaluation. See Text.
NO
2
Bighorn sheep currently occupy the area?
YES
3
Boundaries of bighorn ranges are known?
YES
NO
NO
4
Delineate and buffer core bighorn habitat areas
5
Identify additional restrictions for range boundary determinations including natural and man-made barriers to bighorn movement
6
Probable Bighorn Range Boundaries Well Defined?
NO
7
Refer to text for assistance.
YES
8
Within the potential ranges identified above, deduct unusable portion of habitat as identified in text
9
Adequate Quantity of Range Exists to Support MVPE of Bighorns?
NO
10
Refer to MANAGEMENT DECISION FLOW CHART (See Figure 3)
YES
11
Determine if adequate winter ranges exist to support a MVPE herd by delineating the potential winter range size

Continued on next page

Fig. 2. Part 1: Quantitative Habitat Assessment flow diagram.

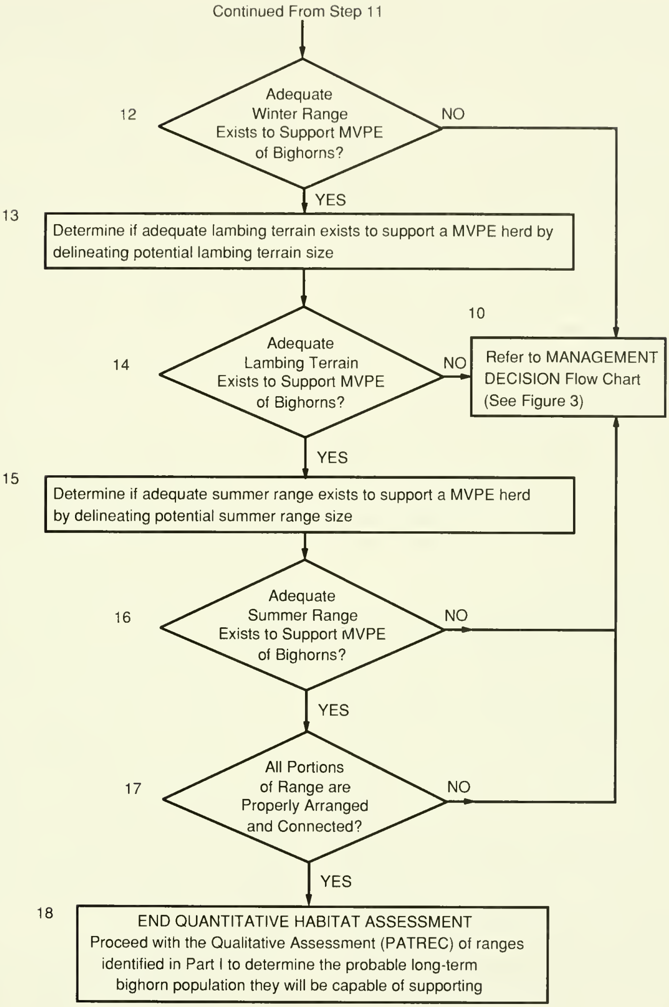

Continued From Step 11
12
Adequate Winter Range Exists to Support MVPE of Bighorns?
NO
YES
13
Determine if adequate lambing terrain exists to support a MVPE herd by delineating potential lambing terrain size
10
Refer to MANAGEMENT DECISION Flow Chart (See Figure 3)
14
Adequate Lambing Terrain Exists to Support MVPE of Bighorns?
NO
YES
15
Determine if adequate summer range exists to support a MVPE herd by delineating potential summer range size
16
Adequate Summer Range Exists to Support MVPE of Bighorns?
NO
YES
17
All Portions of Range are Properly Arranged and Connected?
NO
YES
18
END QUANTITATIVE HABITAT ASSESSMENT
Proceed with the Qualitative Assessment (PATREC) of ranges identified in Part I to determine the probable long-term bighorn population they will be capable of supporting

Fig. 2 continued.

wise useful areas from the rest of the range. As a rule of thumb, although bighorn are adept climbers, if a human cannot negotiate a particular cliff area, bighorn should not be expected to do so either.

4. Valleys or plateaus. If valleys separating areas of escape terrain are wider than 1000 m, they may act as barriers to bighorn movements. Similarly, plateaus separating escape terrain areas by more than 1000 m should be considered range boundary delimiters. When confronted with these barriers, bighorn will attempt to circumvent them if possible. However, if long and continuous, these barriers may totally isolate ranges that otherwise would have value to the herd. In such cases these areas must not be included as bighorn range.

B. Man-made barriers

1. *Water: canals, reservoirs, aqueducts.* Linear waterways generally tend to impede bighorn movements. Concrete-lined canal systems, reservoir impoundments, and aqueduct structures can create impassable barriers and bighorn death traps (Graham 1980). As a general rule, these structures should be considered range delimiters, and bighorn sheep should not be expected to routinely cross them to access other portions of potential range (Sleznik 1963).

2. *Impassable fencing.* Fencing can restrict bighorn movements and result in mortality, particularly for rams whose horns may become entangled. Helvie (1971) presents a useful discussion of the types of fencing that limit bighorn movements. If barrier fencing exists on proposed bighorn ranges, boundaries should be drawn along them.

3. *Major highways and high-use roadways.* Besides the fencing often associated with major highways and high-use roadways (interstate, federal, or state highways), associated human activity often deters bighorn from regularly crossing these areas (Ferrier 1974, McQuivey 1978, Risenhoover 1981, Van Dyke et al. 1983). The impact of highways must be carefully evaluated, and those restricting bighorn movements should be considered boundaries of contiguous bighorn ranges.

4. *Centers of human activity.* Airports, dwellings, campgrounds, and ski resorts are examples of centers of human activity that frequently invade bighorn ranges. As such, they represent potential range delimiters to bighorn sheep, particularly when aligned in linear fashion. Each occurrence must be evaluated individually and range boundaries drawn accordingly.

STEPS 6 AND 7.—Determine whether probable bighorn range boundaries are well defined.

After identifying the above range-delimiting characteristics, managers should roughly define the boundaries of a proposed bighorn sheep release site. If this is not yet possible, given the data to this point, the following additional range constraints should further define range boundaries.

STEP 8.—Deduct unusable portions of habitat from within identified potential bighorn ranges, as follows:

A. Areas beyond 3.2 km from water sources. McQuivey (1978) noted that 85% of bighorn activity occurred within 3.2 km of water. Brundige and McCabe (1986) reported that all bighorn in Custer State Park, South Dakota, remained within 1 km of watering sources. Van Dyke et al. (1983) concluded that water sources farther than 0.5 km from escape terrain received only limited use. Sands (1976) suggested that optimal spacing between water sources was 1.6 km. We believe that critical bighorn ranges will occur within 3.2 km of usable water sources; hence, areas beyond 3.2 km should be excluded from consideration as core-use ranges. It is important to note that seeps, springs, perennial snow patches, streams, rivers, ponds, lakes, and reservoirs all qualify as bighorn watering sources. However, excessive human activity around water resources (Jorgensen 1974), water heavily used by livestock and ungulate wildlife (Welles and Welles 1961, Van Dyke et al. 1983), alkaline waters (Jones et al. 1957), and water sources surrounded by dense vegetation should not be considered usable by bighorn. Schmidt (Colorado Division of Wildlife, personal communications) noted that guzzlers are generally avoided by Rocky Mountain bighorn sheep on Colorado ranges. Having observed the same phenomenon in northeastern Utah, Smith and Flinders (1991) recommended that guzzlers be fitted with remote watering troughs for bighorns to use. In the cooler, temperate regions where the Rocky Mountain subspecies normally occur, water is rarely a limiting factor, unlike areas of desert bighorn habitat to the south. However, where water resources are limited, they must be considered as effective range delimiters.

B. A 100-m-wide buffer should be placed around areas of low to moderate human use. Areas typically receiving low to moderate human activity include some trails, roads, dwellings, and campgrounds. Many have noted the negative effect of human activities on bighorn sheep (Dunaway 1971, Light

1971, Hicks and Elder 1979, Gionfriddo and Krausman 1986). Light (1971) defined "light use" on back-country trails as 0–100 visitors a year, "moderate use" as 100–500 visitors, and "high use" as over 500 visitors a year. He reported that low- to moderate-intensity activity displaced bighorn activity up to 100 m from the source. For this reason these areas should be buffered accordingly.

C. A 150-m-wide buffer around areas of high-intensity human use. Areas typical of high-intensity human activity include some airports, mines, tramways, campgrounds, ski resorts, and heliports. A 150-m-wide buffer beyond the periphery of such areas should be excluded from consideration as bighorn range.

D. All plant communities typified by horizontal visibility of less than 80%. Research by Smith and Flinders (1991), Brundige and McCabe (1986), Risenhoover (1981), and Risenhoover and Bailey (1980) indicates that bighorn avoid areas of poor visibility. Smith and Flinders (1991), using a gridded, meter-square target, measured percentage of target visible in various habitat types and found that bighorn avoid most areas in which horizontal visibility is less than 80%. Conifers with dense understory, brushy meadows, and many riparian areas are of such poor visibility as to preclude bighorn activity. As a rule of thumb, shrub communities with a mean height greater than 0.5 m, riparian areas with a dense understory, heavily forested areas, and more open timber stands with an understory greater than 0.5 m in height will be avoided by bighorn sheep. All such areas should be excluded from the potential bighorn range.

E. Portions of range seasonally occupied by concentrations of elk or cattle. If portions of potential bighorn range will have elk or cattle present concurrently with bighorn, such areas should be excluded from potential bighorn range. Aside from direct competition for forage (McCann 1956, Demarchi 1965, Oldemeyer et al. 1971, Morgan 1973, McQuivey 1978, Estes 1979, Van Dyke et al. 1983), disease transmission (Wishart 1978, Lawson and Johnson 1980, Van Dyke et al. 1983, De Forge 1988, Jessup 1981) and social intolerance (Wilson 1975, McQuivey 1978, Lawson and Johnson 1980, King and Workman 1984) are adequate reasons for excluding elk or cattle ranges from consideration as critical bighorn use areas. That these large ungulates often totally displace bighorn has been well documented; therefore, individual conflicts must be carefully evaluated. Whenever a proposed site will considerably overlap the range of elk, cattle, or perhaps even bison, careful consideration should be given the potential for competition and displacement.

After the areas identified in 8A to 8E have been deducted from potential range defined in steps 4–5, the remaining area represents range suitable for bighorn sheep if introduced into the area. Because transplanted bighorns often establish their home ranges around the release site (Geist 1971, Brundige and McCabe 1986), they can be expected to remain within a 15-mile radius of it once they have adjusted to the area, usually within a year of the release. This may help to further delimit probable ranges in case boundaries are yet ill defined.

STEP 9.—Ascertain whether adequate range exists to support an MVPE of bighorns.

Van Dyke et al. (1983) suggested that 1.9 bighorns per km^2 (5 per mi^2), averaged over an entire range, would represent a maximum density for ranges in the Great Basin portion of southeastern Oregon. If this represents a reasonable estimate for other sites in the Intermountain West, a minimum of 65 km^2 (25 mi^2) of habitat would be required to support 125 bighorn sheep. However, densities ranging from less than 0.4 bighorn per km^2 (1 per mi^2) (McQuivey 1978) to over 27 per km^2 (70 per mi^2) (Demarchi 1965) have been reported. Unfortunately, all reported bighorn densities appear to have been calculated for areas that included both usable and unusable portions of range. This underestimates true bighorn densities within occupied areas. For example, McQuivey (1978) calculated bighorn densities of several Nevada herds using polygons that encircled all observed bighorn sightings. As a result, he included portions of unsuitable ranges with the suitable, thereby overestimating true range size. Demarchi (1965) reported that although the mean density of bighorn for the Chilocotin River area was 4.7 per km^2 (12.1 per mi^2), key grassland areas supported as many as 27 bighorn per km^2 (70.4 per mi^2). In light of these and other research reports, we suggest the following guidelines:

(1) The ranges defined through step 5 (unsuitable portions not yet withdrawn) should not be expected to support more than an average of 3.9 bighorn per km^2 (10 per mi^2). This means that there must be at least 32 km^2 (12.5 mi^2) of habitat identified to the level in step 5 to support at least an MVPE of bighorn sheep.

(2) The ranges remaining after step 8 has been applied (unsuitable portions of range deducted) should not be expected to support more than 7.7 bighorns per km^2 (20 per mi^2). Hence, there must be at least 17 km^2 (6.5 mi^2) of core habitat remaining in order to support at least an MVPE of bighorn sheep.

(3) Proposed ranges with an abundance of grassland can be expected to support more sheep than the above estimates, whereas those with less grassland should be expected to support fewer sheep. However, if range area estimates are not within reasonable boundaries of those recommended above, the site may not warrant a bighorn transplant.

Step 9 instructs wildlife biologists to compare the evaluation area against the minimum range area criteria necessary to support at least 125 sheep. Although these minimum area values are rough estimates, they do represent reasonable minimums and therefore should be seriously considered when potential bighorn reintroduction sites are evaluated. If a proposed release site is so restricted in size that these suggested area minimums cannot be met, the site should not be considered a good candidate for a future release of bighorn sheep. However, as mentioned earlier, another option exists: creating a metapopulation comprising subpopulations of less than 125 bighorn as long as bighorn movements can occur between them.

STEP 10.—Refer to the management decision flow chart.

When a proposed range appears inadequate to support the suggested MVPE of bighorn sheep, the user is referred to the Management Decision Flow Diagram (see Fig. 3, adapted from Holl and Bleich 1982). Figure 3 suggests alternative actions to resolve the problem.

STEP 11.—Determine if adequate winter range exists to support an MVPE herd by delineating the potential winter range size.

Even if a site is satisfactory in all other respects, when winter ranges are inadequate or lacking, a transplant will fail. Indeed, some transplant failures in Utah have been due, in part, to inadequate winter ranges (Smith et al. 1988). Winter ranges are delineated as follows:

A. Select all areas within 300 m of escape terrain. Areas of up to 1000 m from escape terrain may also be included if multiple escape routes exist, as described in step 4.

B. Within areas selected in step 11A, identify sites receiving less than 25 cm of snowpack. Heavy snow accumulations render potential winter range areas unusable (McCann 1956, Tilton and Willard 1982, Johnson 1983, Smith and Flinders 1991). Research in northeastern Utah indicated that bighorns abandoned ranges when snowpack exceeded 25 cm.

C. Of those areas selected in step 11B, exclude all escape terrain without southern exposures (SW-S-SE). Studies addressing winter range requirements have consistently noted that key winter ranges are typified by southern exposures (Shannon et al. 1975, Hudson et al. 1976, Stelfox 1976, Johnson 1983, Smith and Flinders 1991). Identify those areas.

D. Determine the total area of potential winter range from those areas that fit the criteria in steps 11A–C. Add the areas and calculate the total area of probable winter range available.

STEP 12.—Verify whether adequate winter range exists to support an MVPE of bighorns.

Step 12, like step 9, alerts site evaluators to critical winter range deficiencies. How much winter range is adequate? Coggins (1980) reported winter range densities of 31 bighorns per km^2 (80 per mi^2) for the Lostine River herd of northeast Oregon. Woodgerd (1964) and Blood (1963) reported winter range densities of 19–23 bighorns per km^2 (50 to 60 per mi^2). Wehausen (1983) reported winter densities averaging 20 bighorns per km^2 (52 per mi^2) for the Mt. Baxter herd. High-quality portions of the same winter ranges supported nearly double the average value, or 37 big-

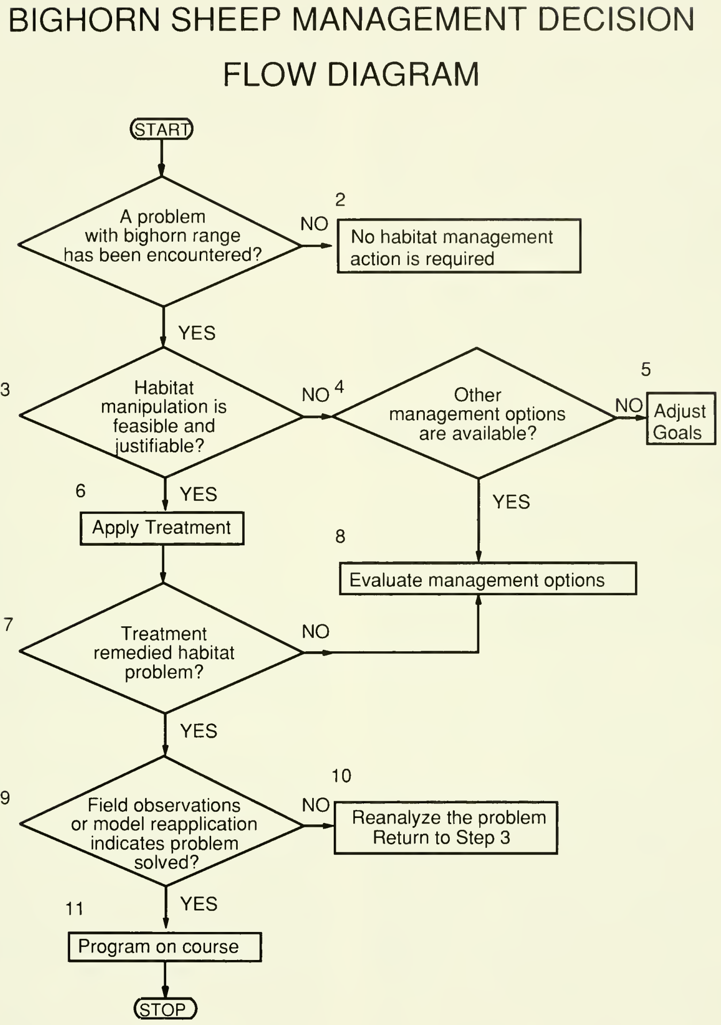

BIGHORN SHEEP MANAGEMENT DECISION FLOW DIAGRAM
START
1
A problem with bighorn range has been encountered?
NO
2
No habitat management action is required
YES
3
Habitat manipulation is feasible and justifiable?
NO
4
Other management options are available?
NO
5
Adjust Goals
6
YES
Apply Treatment
YES
8
Evaluate management options
7
Treatment remedied habitat problem?
NO
YES
9
Field observations or model reapplication indicates problem solved?
NO
10
Reanalyze the problem Return to Step 3
11
YES
Program on course
STOP

Fig. 3. Bighorn Sheep Management Decision flow diagram.

horn per km^2 (97 per mi^2). In light of these and other reports, we believe that winter ranges should not be expected to support more than 20 bighorns per km^2 (about 50 per mi^2). Therefore, to sustain an MVPE of 125 bighorns, a particular range must have at least 6.5 km^2 (2.5 mi^2) of available winter range. If an analysis of this step reveals inadequate winter range, then refer to the Management Decision Flow Diagram (Fig. 3), which recommends alternative actions to resolve the problem.

STEP 13.—Determine if adequate lambing terrain exists to support an MVPE herd by delineating potential lambing terrain size.

In some instances, inadequate quantities of lambing terrain have been cited as the ultimate factor controlling bighorn herd size (Hansen 1982). The importance of adequate amounts of suitable lambing terrain cannot be overemphasized, as lamb survival and recruitment can have a greater effect upon transplant success than any other factor of herd population dynamics (Smith and Flinders 1991). Lambing terrain has been defined as the most precipitous, rugged, and remote areas of the bighorn ranges; in addition, these areas are near forage and have dry, southern exposures (Geist 1971, Van Dyke et al. 1983). Identify and select those areas meeting the following criteria:

A. Select all areas identified as potential escape terrain. These areas have already been identified in step 4.

B. Of areas identified in step 13A, select all southerly aspects. Lambing areas most commonly have southern exposures (Geist 1971, Van Dyke et al. 1983, Smith and Flinders 1991). Smith and Flinders (1991) indicated that most lambing areas fall within aspects from 90° to 270°. Select escape terrain areas that fit these aspect criteria.

C. Of areas identified in step 13B, select those typified by horizontal visibility of greater than 80%. Refer to step 8D for a discussion and description of the concept of horizontal visibility. Visibility is measured along predator-approach pathways, not into, or over, cliffs. Because bighorns consistently select against areas having poor visibility, only areas of good visibility are considered suitable for lambing.

D. Of areas identified in step 13C, select only portions within 1000 m of usable water sources. Because of the water demands of lactating ewes, and the inability of young lambs to travel far, water sources need to be within, or adjacent to, lambing areas (Van Dyke et al. 1983). Smith and Flinders (1991) suggest a maximum distance from water of 675 m. Beyond that distance use of lambing terrain declines rapidly. For purposes of this evaluation, areas beyond 1000 m from water should not be considered usable for lambing.

E. Deduct from areas identified in step 12D habitats that are smaller than 2 ha (5 acres). Van Dyke et al. (1983) suggest that ewes select rugged cliffs that are greater than 2 ha for lambing. They did say, however, that if an area is remote, extremely rugged, and free of harassment, parcels as small as 1 ha (2.5 acres) receive occasional use. For purposes of this assessment, areas less than 2 ha should not be considered potential lambing terrain unless extremely rugged and isolated.

F. Determine the total hectares of potential lambing terrain from areas meeting the criteria of steps 13A–E. Sum the areas of probable lambing terrain identified in steps 13A–E.

STEP 14.—Decide if adequate lambing terrain exists to support an MVPE of bighorns.

As in steps 9 and 12, step 14 warns biologists of proposed release sites that are deficient in critical lambing terrain. Although reported bighorn age/sex ratios vary widely, an MVPE population of 125 should have approximately 50–60 breeding ewes (inferred from data from Buechner 1960, Oldemeyer et al. 1971, Holl 1982, McQuivey 1978, Smith et al. 1988). Holl (1982) showed that 60 ha of escape terrain is needed to support 10 lambing ewes. If this assumption is true for bighorn in the Intermountain West, a minimum of 300–360 ha (1.2–1.4 mi^2) of suitable escape terrain would be required to support the 50–60 ewes during lambing. It is recommended that at least 360 ha (1.4 mi^2) of escape terrain, as classified in steps 13A–F, be available for lambing. If the available lambing terrain is less than the recommended baseline value of 360 acres, refer to the Management Decision Flow Diagram for suggested alternative actions.

STEP 15.—Determine if adequate summer range exists to support an MVPE herd by delineating potential summer range areas.

In some instances, inadequate quantities of summer range have been cited as the key factor limiting bighorn herd size (Arnett et al. 1990). Summer ranges, as defined here, refer to those areas utilized by all bighorns not involved in lambing activities from May through August. This nonlambing group includes the mature ram cohort (four-year-olds and older), yearlings, two-year-old ewes, young rams up to three years of age, and barren ewes. While these sheep are occupying summer ranges, ewes inhabit lambing ranges. Identify and select those areas meeting the following criteria:

A. Delimit all buffer areas (300 m) adjacent to, but not including, escape terrain. These areas were identified in step 4. They include areas having slopes less than 60%.

B. Of areas identified in step 15A, select those having horizontal visibility greater than 80%. Refer to step 8D for a discussion of the concept of horizontal visibility. Bighorns avoid areas of poor visibility; thus, areas of high visibility should be selected as suitable for summer range.

C. Of areas identified in step 15B, select only portions within 3.2 km of water. As discussed in step 8A, it is assumed that ranges farther than 3.2 km from water do not constitute key areas for sheep and are thus withdrawn from consideration as summer range.

D. Determine the total hectares of potential summer range from areas meeting the criteria in steps 15A–C. Calculate the total area of probable summer ranges as identified in steps 15A–C.

STEP 16.—Insure that adequate summer range exists to support an MVPE of bighorns.

As with steps 9, 12, and 14, step 16 alerts biologists to sites deficient in summer range. As discussed above, an MVPE population of 125 would have approximately 50–60 breeding ewes at most. This leaves approximately 65–75 nonbreeding bighorn to occupy summer ranges. In step 9 it was suggested that ranges would probably not support more than 7.7 bighorns per km^2 (20 per mi^2). Therefore to support 65–75 bighorns on summer range, at least 8.4–9.7 km^2 (3.2–3.6 mi^2) of summer range should be available. If available summer rangelands are significantly less than these recommended areas, consult the Management Decision Flow Diagram for alternatives.

STEP 17.—Determine whether all portions of range are properly arranged and connected.

The quantity, quality, and juxtaposition of forage, water, and escape terrain interact to determine bighorn population size and health (Hansen 1982, Van Dyke et al. 1983). In optimum bighorn habitats, water sources and escape terrain are interspersed throughout forage areas. This interspersion promotes herd dispersal and protects the range against overuse of plant communities. If escape terrain, water, and forage are not intermixed throughout the bighorn range, the situation is not ideal. If other critical elements of bighorn ranges are deficient (total area available, area of winter range, lambing terrain, or summer range), the area being evaluated may not be suitable for bighorn reintroduction unless management actions can correct the problems.

STEP 18.—This concludes Part 1 of the Rocky Mountain Bighorn Sheep Habitat Evaluation Procedure. If insurmountable habitat problems were encountered in Part 1, further evaluation (application of Part 2) of the proposed bighorn sheep ranges is unnecessary. If, however, the ranges appear to satisfy the foregoing minimum criteria, habitat quality estimation may be desirable. For range quality analysis proceed to Part 2 of this HEP.

Part 2

Qualitative Assessment of Available Bighorn Habitat—PATREC

Once bighorn range boundaries have been determined, an estimate of range quality may follow. A range that is capable of supporting an MVPE of bighorns must fulfill the continuously changing needs of herd members (Holl and Bleich 1982). Because varying seasonal demands accompany each bighorn cohort (ram and ewe superclass), three separate PATREC models have been constructed: (1) a ram spring-summer model, (2) a ewe spring-summer (lambing period) model, and (3) an all bighorn fall-winter model (Tables 1–3). These three models permit analysis of the habitat from the unique perspective of each group. Because Bear Mountain ram and ewe cohorts did not sufficiently segregate after the fall rut season, a single model was used to analyze habitat.

A map that estimates bighorn density for the site can be constructed from PATREC models. This density map presents changing

TABLE 1. Habitat evaluation model (PATREC) for spring-summer bighorn ram ranges of northeastern Utah [prior probabilities P(H) = High = .30; P(L) = Low = .70].

Habitat attributes	Conditional probabilities High	Low
TERRAIN		
1. The area is greater than, or equal to, 7250′ elevation.	0.78	0.30
2. The average slope of the area is:		
a. less than 6°.	0.67	0.20
b. 6° to 15°.	0.22	0.20
c. greater than 15°.	0.11	0.60
3. The area is not within escape terrain.	0.89	0.40
VEGETATION		
4a. The area has horizontal visibility greater than, or equal to, 90%.	0.67	0.10
OR		
4b. Tree canopy cover is less than, or equal to, 10%.	0.89	0.60
OR		
4c. Average shrub height is less than, or equal to, 0.5 meters.	0.67	0.40
5. Grass, forb, and shrub cover is greater than, or equal to, 15%.	0.67	0.10
6. The area supports greater than, or equal to, 250 kg per hectare (dry weight) of grasses and forbs.	0.78	0.33

TABLE 2. Habitat evaluation model (PATREC) for spring-summer bighorn ewe lambing ranges of northeastern Utah [prior probabilities P(H) = High = .30; P(L) = Low = .70].

Habitat attributes	Conditional probabilities High	Low
TERRAIN		
1. The area is less than, or equal to, 6400′ elevation.	0.67	0.44
2. The average slope of the area is:		
a. less than 35°.	0.11	0.33
b. 35° to 40°.	0.77	0.01
c. greater than 40°.	0.12	0.66
3. More than 75% of the area has aspects between 180° and 270° from north.	0.67	0.11
4. The area is within 100 meters of water source.	0.78	0.33
VEGETATION		
5a. Tree canopy cover is less than, or equal to, 6%.	0.55	0.33
OR		
5b. The area has horizontal visibility greater than, or equal to, 80%.	0.77	0.99
6. The area has shrub cover less than, or equal to, 6%.	0.99	0.43

habitat quality across the site, indicating areas of higher and lesser value to sheep. This implies that once bighorn introduced to the area reach a carrying capacity equilibrium, PATREC predictions will approximate actual density distributions. There has been debate about the use of density as an indicator of habitat quality (Van Horne 1983, Maurer 1986). However, it is believed that bighorn sheep respond numerically to habitat quality such that increasing numbers of animals occupy sites of increasing quality (Smith and Flinders 1991).

It is important to note that Part 2 of this procedure has been specifically developed with data obtained from the Bear Mountain bighorn herd. Managers should recognize that some habitat-related questions may not be applicable to sites other than the Bear Mountain area. However, because each specific PATREC question addresses a habitat variable important to bighorn sheep, managers should attempt to obtain accurate values for these variables before conducting a PATREC analysis. Replacement of PATREC values reported here with more appropriate ones from local situations is not that difficult. For example, in Table 1, habitat attribute 1 indicates that 7250′ elevation is a break-point for observed bighorn densities. The assigned probabilities indicate that 78% of the time high densities of rams were observed above 7250′, whereas low densities of rams occurred at or above that elevation only 30% of the time. The 7250′-elevation contour corresponds to the canyon rim at Bear Mountain, a steep-sided plateau. Above 7250′ bighorn rams utilize the relatively level rim areas, typified by slopes of less than 6° and abundant forage. With little reason to use the steep, less productive cliff areas, rams occur in higher numbers on the rim. Concurrently, driven by behavior to protect their newborn lambs, ewes are found mostly at lower elevations (in cliffs) typified by very steep slopes (35°-40°) (Table 2). Because many transplant sites have similar elevational break-points between precipitous escape terrain and the more level, high-productivity forage areas, managers can

TABLE 3. Habitat evaluation model (PATREC) for fall-winter bighorn ranges of northeastern Utah [prior probabilities P(H) = High = .30; P(L) = Low = .70].

	Conditional probabilities	
Habitat attributes	High	Low
TERRAIN		
1. The area is greater than, or equal to, 7000′ elevation.	0.90	0.20
2. The average slope of the area is:		
a. less than 6°.	0.60	0.20
b. 6° to 15°.	0.30	0.01
c. greater than 15°.	0.10	0.79
3. The area is within 275 meters of, but not in, escape terrain.	0.80	0.10
VEGETATION		
4a. Tree canopy cover is less than, or equal to, 5%.	0.90	0.40
OR		
4b. The area has horizontal visibility greater than, or equal to, 90%.	0.90	0.40
OR		
4c. Average shrub height is less than, or equal to, 0.4 meters.	0.90	0.40
5. Grass and forb cover is greater than, or equal to, 14%.	0.70	0.20
6. The area supports greater than, or equal to, 300 kg per hectare (dry weight) of grasses and forbs.	0.80	0.10

reasonably substitute those values. Also, note that each of the three PATREC submodels has several habitat attributes separated by the word "or." Because an underlying assumption of Bayes Theorem is that all habitat attributes are independent, those found to be interdependent are separated by "or," giving the user the option of selecting one of the listed alternatives, allowing for flexibility in the database.

PATREC analysis requires detailed, site-specific information and is tedious to conduct by hand. Manual application (i.e., noncomputer assisted) of PATREC models for wildlife has been successfully conducted for very large areas with satisfying results (Evans 1983, Wilson 1983). However, current GIS computer technology can be successfully employed to perform these same analyses in significantly less time and with much less effort. We fully recommend the GIS approach to PATREC analysis; however, an overview of both approaches is presented here for the benefit of those with, and without, GIS computer technology.

It is beyond the scope of this paper to discuss the intricacies of PATREC modeling. Therefore, a thorough review of Kling (1980), Evans (1983), or Wilson (1983) is essential, as each of these references contains detailed information regarding the theory, methodology, application, and utility of PATREC models for wildlife. The primary purpose of this section is to present an existing bighorn PATREC model, its application, and utility.

Because the manual and GIS computer approaches to PATREC model application differ widely, each is addressed separately. The following discussion is based on the stepwise procedure outlined in Figure 4. The numbers to the left of each step uniquely identify it and will be referred to below.

The Manual PATREC Model Approach

STEP 1.—Because PATREC models cannot be applied to an entire bighorn range simultaneously, available bighorn habitat (defined in Part 1) must be subdivided into PATREC model evaluation units (MEU) for the analysis of habitat quality. Once subdivided, each of the analysis subunits is individually evaluated. A subunit of 16.2 ha (40 acres) is suggested, although biologists can adjust the MEU's area as needs dictate. However, as MEU size increases, model resolution will become coarser; and important, high-quality portions of range may go unidentified or be downgraded as they are averaged with adjacent areas of lesser quality. Mylar overlays on topographic maps can provide the necessary analysis grid of MEUs. A data sheet should be constructed that contains a unique label for referencing each MEU and its associated PATREC posterior probabilities.

STEPS 2 AND 3.—Each MEU should be evaluated using each of the three submodels (Tables 1–3). If a user suspects that lambing terrain may be inadequate, he may choose to apply only that PATREC submodel while omitting the other two.

Subunit evaluations compare each subunit's habitat attributes with those listed in the PATREC models. If the subunit meets the criteria of each habitat attribute, then the high- and low-conditional probabilities

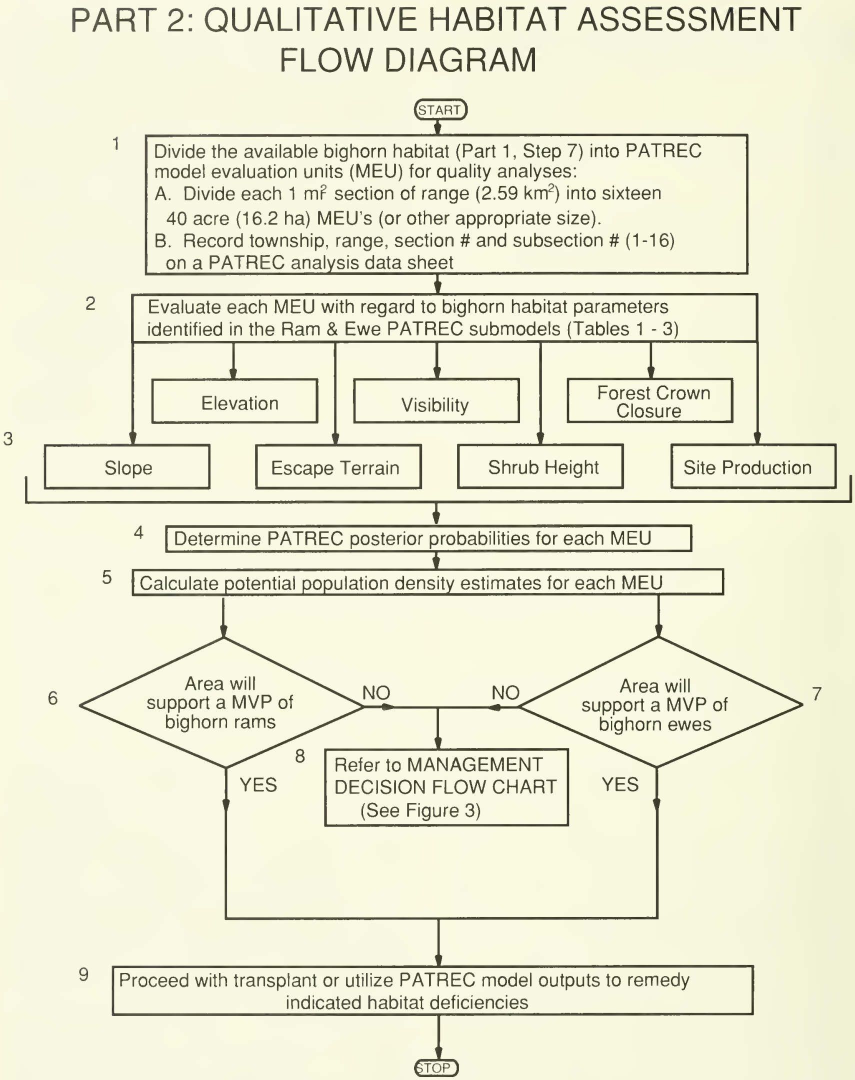

PART 2: QUALITATIVE HABITAT ASSESSMENT FLOW DIAGRAM
START
1
Divide the available bighorn habitat (Part 1, Step 7) into PATREC model evaluation units (MEU) for quality analyses:
A. Divide each 1 mi² section of range (2.59 km²) into sixteen 40 acre (16.2 ha) MEU's (or other appropriate size).
B. Record township, range, section # and subsection # (1-16) on a PATREC analysis data sheet
2
Evaluate each MEU with regard to bighorn habitat parameters identified in the Ram & Ewe PATREC submodels (Tables 1 - 3)
Elevation
Visibility
Forest Crown Closure
3
Slope
Escape Terrain
Shrub Height
Site Production
4
Determine PATREC posterior probabilities for each MEU
5
Calculate potential population density estimates for each MEU
6
Area will support a MVP of bighorn rams
NO
NO
Area will support a MVP of bighorn ewes
7
8
Refer to MANAGEMENT DECISION FLOW CHART (See Figure 3)
YES
YES
9
Proceed with transplant or utilize PATREC model outputs to remedy indicated habitat deficiencies
STOP

Fig. 4. Part 2: Qualitative Habitat Assessment flow diagram.

associated with each are used in calculation of the site's overall high- and low-density probabilities. When habitat attribute criteria are not met by the site, each high- and low-conditional probability is subtracted from 1 and the result recorded for use in subsequent calculations.

STEP 4.—PATREC model outputs are expressed as probabilities. These probabilities express the likelihood that the evaluated parcel of range (MEU) will support a high-density population and the probability it will support a low-density population. Computations to provide these outputs are quite simple and can be done by hand, though not recommended, or with a hand-held calculator or a computer. Once the required inventory data are gathered from an MEU and compared with habitat attribute criteria, the resulting conditional probabilities P(ID/H) and P(ID/L) are used in Bayes Theorem as follows:

$$P(H/ID) = \frac{P(H) \times P(ID/H)}{P(H) \times P(ID/H) + (P(L) \times P(ID/L)}$$

where P(H/ID) is the probability that the area will support a high-density population based on inventory data. P(H) and P(L) are the probabilities of a high- or low-density area (prior probabilities) naturally occurring. Every subunit has an associated probability of supporting a high density and a low density of bighorn sheep. Since these two probabilities must sum to 1, 1 minus the high-density probability yields the low-density probability. For all three PATREC models the prior probabilities for high and low have been assigned the values of 0.30 and 0.70, respectively. This assignment of values is a reflection of the relative abundance of habitats in northeastern Utah capable of supporting high- and low-density bighorn sheep populations. This implies that a random sample of habitat would select high-density types 3 times out of 10 and low-density types 7 out of 10. These probabilities do not address land beyond the delineated bighorn range boundaries. These values can, and should, be changed to local situations when the proportion of high to low habitat is clearly different. In situations where the proportion is unknown, assigning probabilities of 0.50 to each cancels out the effects of this variable's input on the model (see Kling 1980 for further discussion). P(ID/H) and P(ID/L) represent the probabilities that the inventory data have a high- or low-density potential, respectively (conditional probabilities). An example here will illustrate how Bayes Theorem is used.

Suppose a particular MEU was evaluated and only habitat attributes 2A, 6, and 7 of the spring-summer bighorn ram model (Table 1) were satisfied. The probability of the site providing high-density habitat for bighorn rams, given those inventory data, is then calculated. It should be noted that when habitat criteria are not satisfied by the site (numbers 1, 3, 4C, and 5), both high- and low-conditional probabilities are subtracted from 1. To illustrate, the necessary calculations are performed:

$$\begin{aligned} P(ID/H) &= \text{(product of all seven attributes' high probabilities multiplied)} \\ P(ID/H) &= (1-.78)(.67)(1-.89)(1-.67)(1-.67)(.67)(.78) \\ &= 0.000922757 \\ P(ID/L) &= \text{(product of all seven attributes' low probabilities multiplied)} \\ P(ID/L) &= (1-.30)(.20)(1-.30)(1-.40)(1-.10)(.01)(.33) \\ &= 0.000174636 \end{aligned}$$

These conditional probabilities are then substituted into the Bayes Theorem as follows:

$$\begin{aligned} P(H/ID) &= \frac{(0.3)(0.000922757)}{(0.3)(0.000922757)+(0.7)(0.000174636)} \\ &= 0.69 \\ P(L/ID) &= 1.0 - 0.69 = 0.31 \end{aligned}$$

From these inventory data, we can conclude that the probability of the area supporting a high density of bighorn sheep is 0.69, or 69%. Conversely, the probability that the same area would support a low-density population is 0.31 or 31%.

STEP 5.—As discussed in step 8 of Part 1, bighorn population densities ranging from less than 0.4 bighorn per km^2 (1 per mi^2) (McQuivey 1978) to over 27 per km^2 (70 per mi^2) (Demarchi 1965) have been reported. For the sake of this model it is assumed that low-density habitat will support 1.0 bighorn per km^2 and high-density habitat will support 25 bighorn per km^2. Based on those density estimates, PATREC predicts that the MEU will support (0.69)(25 bighorn/km^2), or 17 bighorns per km^2, when the population is at, or near, its carrying capacity.

STEPS 6 AND 7.—Because PATREC outputs can be translated into the long-term population densities that a range can be expected to support (discussed in step 5), the number of rams and ewes that an area may be expected to support can be calculated. Although the percent composition of rams, ewes, yearlings, and lambs varies from herd to herd, it is recommended that ram habitat be able to support at least 25 adult rams (four years old and older), and the ewe habitat at least 100 members of the ewe super-class (all ewes, yearlings, and lambs).

STEP 8.—If the PATREC model reveals deficiencies, management may choose to focus on each deficiency individually. The Management Decision Flow Diagram guides decision making in those instances.

STEP 9.—PATREC models also provide some insight as to what management could do to improve the area for bighorn sheep. In the above example, there is little that can be done about habitat attributes 1 (elevation) or 3 (amount of escape terrain), but 4C and 5 (shrub height and herbaceous vegetation cover) could be managed so that the probability of the area supporting a larger population could be increased. By trying various "What if?" scenarios, managers can also identify alternative habitat modifications most likely to have high cost/benefit returns. For instance, if managers were to alter shrub height by burning and thereby satisfy attribute 4C, the resultant P(H/ID) is 0.87, for a net increase in habitat suitability of 18%. However, if managers had chosen to alter attribute 5 instead by increasing the total herbaceous plant cover, the resulting probability that the site will be capable of supporting a high-density population would have increased to 0.98, giving a net increase of 29%. Once the differential in cost is calculated for each scenario, the plan of action that will return the most per unit effort invested will be apparent.

The GIS Computer PATREC Model Approach

No flow diagram has been provided for the GIS computer PATREC model approach. However, the following discussion should assist the reader in understanding an overview of the process.

As with the manual method, the entire bighorn range must be analyzed with each of the PATREC submodels for accurate habitat assessment. The GIS approach circumvents the need for subdividing the evaluation site into analysis units and thereby avoids the tedium associated with it. Instead, the habitat requirements specified by each submodel are used to identify qualifying portions of the GIS data base. For example, the ram spring-summer PATREC submodel (Table 1) indicates in habitat attribute 1 that elevations above and below 7250′ are important in determining habitat suitability. For this elevational attribute, the user would access the digital elevation map and reclassify it into only two categories: those above 7250′ and those below 7250′ elevation. Secondly, all areas (polygons) within each category would be encoded with the appropriate conditional probabilities, as presented in Table 1. Because areas below 7250′ elevation do not meet the given habitat criteria, they are labeled with 1 minus the given probabilities. In a like manner, the user proceeds to subdivide the GIS data base according to each of the habitat criteria listed, labeling each newly created category of polygons with the appropriate conditional probability values. Finally, all polygons are merged to create a composite map comprised of the intersection of all habitat attributes and associated probabilities. The GIS creates a new table for each polygon containing an entire listing of the conditional probabilities associated with its particular habitat attributes, as specified by the PATREC submodels. A composite map of these merged polygons is created independently for each submodel.

The information stored in the relational data base for each range polygon is used to calculate resultant probabilities using Bayes Theorem, as demonstrated above. Fortunately, many GIS applications have the ability to access the stored values, perform these time-consuming calculations for each subunit, and return the results, i.e., probabilities, for each polygon. The GIS can then use these resultant probabilities to calculate estimates of bighorn densities for each polygon. As in the manual method, the total number of sheep the site is capable of supporting is determined by summing the estimated density values for all polygons. These individual values (i.e., number of rams in spring-summer, number of ewes during lambing, etc.) must exceed those presented above in step 6 of the Manual PATREC approach. In this manner, seasonal/cohort weaknesses of a site are identified, and management can focus on the real problem areas. GIS utility and power streamline the PATREC process immensely and put within reach of many this powerful tool for habitat quality evaluation.

This concludes application of Part 2 of the bighorn HEP. Upon completion of bighorn habitat evaluation, the investigator should know whether or not an evaluated site could support reintroduced bighorn sheep and what could be done in the event limiting factors need attention.

CONCLUSIONS

Although efforts have been underway for several decades to reestablish Rocky Mountain bighorn sheep to formerly occupied ranges, many transplant efforts have failed. In order for Utah, and other western states, to have a more successful reintroduction program, a rigorous, biologically based habitat assessment procedure has been devised. It is hoped that this procedure will help managers avoid "doomed-from-the-start" reintroductions and greatly enhance transplant success.

ACKNOWLEDGMENTS

We wish to thank the Utah Division of Wildlife Resources, the U.S. Forest Service, Brigham Young University, and the Bureau of Land Management for generous support of the Bear Mountain bighorn research project. Thanks are due Dr. Perry Hardin of the Geography Department at Brigham Young University for his GIS expertise and assistance. We also extend special appreciation and recognition to Bob Nielson for his love of wildlife and vision of bighorn restoration to former Utah ranges.

LITERATURE CITED

ARMENTROUT, D. J., AND W. R. BRIGHAM. 1988. Habitat suitability rating system for desert bighorn sheep in the Basin and Range Province. USDI Bureau of Land Management Technical Note 384. 18 pp.

ARNETT, E. B., F. G. LINDZEY, AND L. L. IRWIN. 1990. Use of clearcuts by Rocky Mountain bighorn sheep in south-central Wyoming. Biennial Symposium of the Northern Wild Sheep and Goat Council. In press.

BERGER, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conservation Biology 1: 91–98.

BLOOD, D. A. 1963. Some aspects of behavior of a bighorn herd. Canadian Field Naturalist 77: 77–94.

BROWN, G. W. 1974. Distribution and population characteristics of bighorn sheep near Thompson Falls in northwestern Montana. Unpublished master's thesis, University of California at Riverside. 133 pp.

BRUNDIGE, G. C., AND T. R. MCCABE. 1986. Summer habitat use by bighorn ewes and lambs. Biennial Symposium of the Northern Wild Sheep and Goat Council 5: 408–420.

BUECHNER, H. K. 1960. The bighorn sheep in the United States, its past, present and future. Wildlife Monographs 4. 174 pp.

CAPURRO, W. N. 1988. Entire California bighorn herd dies in the Warner Mountains. Page 65 *in* Wild sheep, official publication of the Foundation for North American Wild Sheep. Summer issue.

COGGINS, V. L. 1980. Present status of Rocky Mountain bighorn sheep in northeast Oregon. Biennial Symposium of the Northern Wild Sheep and Goat Council 2: 90–104.

COWAN, I. M. 1940. Distribution and variation in the native sheep of North America. American Midland Naturalist 24: 505–580.

DEMARCHI, R. A. 1965. An ecological study of the Ashnola bighorn winter ranges. Unpublished master's thesis, University of British Columbia, Vancouver. 103 pp.

DUNAWAY, D. J. 1971. Human disturbance as a limiting factor of Sierra Nevada bighorn sheep. Pages 165–173 *in* E. Decker, ed., Transactions of the First North American Wild Sheep Conference. Colorado State University, Department of Fish and Wildlife Biology, Fort Collins.

EVANS, L. C. 1983. Impact assessment and mitigation planning with habitat evaluation models. Unpublished master's thesis, Colorado State University, Fort Collins. 299 pp.

FERRIER, G. J. 1974. Bighorn sheep along the lower Colorado River. Desert Bighorn Sheep Council Transactions 18:40–45.

FERRIER, G. J., AND W. G. BRADLEY. 1970. Bighorn habitat evaluation in the Highland Range in southern Nevada. Desert Bighorn Sheep Council Transactions 14: 69–93.

FOREYT, W. J. 1988. Fatal *Pasteurella haemolytica* pneumonia in bighorn sheep following direct contact with normal domestic sheep: an experimental study. Biennial Symposium of the Northern Wild Sheep and Goat Council 6: 65.

______. 1990. Pneumonia in bighorn sheep: effects of *Pasteurella haemolytica* from domestic sheep and effects on survival and long-term reproduction. Biennial Symposium of the Northern Wild Sheep and Goat Council. In press.

GEIST, V. 1971. Mountain sheep, a study in behavior and evolution. University of Chicago Press, Chicago. 383 pp.

______. 1975. On the management of mountain sheep: theoretical considerations. Pages 77–98 *in* J. B. Trefethen, ed., The wild sheep of modern North America. Boone and Crockett Club, Alexandria, Virginia. 302 pp.

______. 1988. How markets in wildlife meat and parts, and the sale of hunting privileges, jeopardize wildlife conservation. A paper presented at the 1988 Wildlife Society meeting, held 24–25 February 1988, Provo, Utah. 42 pp.

GIONFRIDDO, J. P., AND P. R. KRAUSMAN. 1986. Summer habitat use by mountain sheep. Journal of Wildlife Management 50: 331–336.

GOLDEN, H., AND G. K. TSUKAMOTO. 1980. Potential bighorn sheep habitat in northern Nevada. A contract study for the Bureau of Land Management by the Nevada Department of Wildlife, Reno. 100 pp.

Goodson, N. J. 1982. Effects of domestic sheep grazing on bighorn sheep populations: a review. Biennial Symposium of the Northern Wild Sheep and Goat Council 3: 287–313.

Graham, H. 1980. The impact of modern man. Pages 288–309 *in* G. Monson and L. Sumner, eds., The desert bighorn—its life history, ecology, and management. University of Arizona Press, Tucson.

Grubb, T. G. 1988. Pattern recognition—a simple model for evaluating wildlife habitat. USDA Forest Service Research Note RM-87. 5 pp.

Grunigen, R. E. 1980. A system for evaluating potential bighorn sheep transplant sites in northern New Mexico. Biennial Symposium of the Northern Wild Sheep and Goat Council 2: 211–228.

Hansen, C. G. 1980. Habitat evaluation. Pages 320–335 *in* G. Monson and L. Sumner, eds., The desert bighorn—its life history, ecology, and management. University of Arizona Press, Tucson. 370 pp.

Hansen, M. C. 1982. Status and habitat preference of California bighorn sheep on the Sheldon National Wildlife Refuge. Unpublished master's thesis. Oregon State University, Corvallis. 47 pp.

_____. 1984. Population growth and dispersal of reintroduced California bighorn in northwestern Nevada. Cal-Neva Wildlife Society Transactions, pp. 43–49.

Helvie, J. B. 1971. Bighorns and fences. Desert Bighorn Sheep Council Transactions 15: 53–62.

Hicks, L. L., and J. M. Elder. 1979. Human disturbance of Sierra Nevada bighorn sheep. Journal of Wildlife Management 43: 909–915.

Holl, S. A. 1982. Evaluation of bighorn sheep habitat. Desert Bighorn Sheep Council Transactions 26: 47–49.

Holl, S. A., and V. C. Bleich. 1982. San Gabriel mountain sheep: biological and management considerations. USDA Forest Service, San Bernardino National Forest. 120 pp.

Hudson, R. J., D. M. Hebert, and V. C. Brink. 1976. Occupational patterns of wildlife on a major East Kootenay winter-spring range. Journal of Range Management 29:38–42.

Jahn, L. R., and J. B. Trefethen. 1978. Funding wildlife conservation programs. Pages 456–470 *in* H. P. Brokaw, ed., Wildlife and America—contributions to an understanding of American wildlife and its conservation. Council on Environmental Quality, Washington, D.C.

Jessup, D. M. 1981. Pneumonia in bighorn sheep: effects on populations. Cal-Neva Wildlife Society Transactions, pp. 72–78.

Johnson, R. L. 1983. Mountain goats and mountain sheep of Washington. Washington Department of Game, Biological Bulletin No. 18. 196 pp.

Jorgensen, P. 1974. Vehicle use at desert bighorn watering area. Desert Bighorn Sheep Council Transactions 18:18–24.

King, M. M., and G. M. Workman. 1984. Cattle grazing in desert bighorn sheep habitat. Desert Bighorn Sheep Council Transactions 28: 18–22.

Kling, C. L. 1980. Pattern recognition for habitat evaluation. Unpublished master's thesis. Colorado State University, Fort Collins. 244 pp.

Light, J. T. 1971. An ecological view of bighorn habitat on Mt. San Antonio. Pages 150–157 *in* E. Decker, ed., Transactions of the First North American Wild Sheep Conference, Colorado State University, Department of Fish and Wildlife Biology, Fort Collins. 187 pp.

Maurer, B. A. 1986. Predicting habitat quality for grassland birds using density-habitat correlations. Journal of Wildlife Management 50: 556–566.

McCann, L. J. 1956. Ecology of the mountain sheep. American Midland Naturalist 56:297–324.

McQuivey, R. P. 1978. The desert bighorn of Nevada. Biological Bulletin No. 6. Nevada Department of Wildlife, Reno. 81 pp.

Merritt, M. F. 1974. Measurement of utilization of bighorn sheep habitat in the Santa Rosa Mountains. Desert Bighorn Sheep Council Transactions 18: 4–17.

Oldemeyer, J. L., W. J. Barmore, and D. L. Gilbert. 1971. Winter ecology of bighorn sheep in Yellowstone National Park. Journal of Wildlife Management 35:257–269.

Risenhoover, K. L. 1981. Winter ecology and behavior of bighorn sheep, Waterton Canyon, Colorado. Unpublished master's thesis. Colorado State University, Fort Collins. 107 pp.

Risenhoover, K. L., and J. A. Bailey. 1980. Visibility: an important factor for an indigenous, low-elevation bighorn herd in Colorado. Biennial Symposium of the Northern Wild Sheep and Goat Council 2: 18–28.

Sands, A. R. 1976. Evaluation of potential California bighorn sheep habitat, Jackson Mountains, Nevada. Unpublished master's thesis, Humboldt State University, Arcata, California. 104 pp.

Schwartz, O. ,V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. Biological Conservation 37: 179–190.

Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. International Conference on Bear Research and Management 5: 133–139.

Shannon, N. H., R. J. Hudson, V. C. Brink, and W. D. Kitts. 1975. Determinants of spatial distribution of Rocky Mountain bighorn sheep. Journal of Wildlife Management 39:387–401.

Sleznik, J., Jr. 1963. The bighorn sheep of Lake Mead National Recreation Area. Desert Bighorn Council Transactions 7:58–60.

Smith, T. S., and J. T. Flinders. 1991. The bighorn sheep of Bear Mountain: ecological investigations and management recommendations. Utah Division of Wildlife Resources, research final report. 425 pp.

Smith, T. S., J. T. Flinders, and D. W. Olsen. 1988. Status and distribution of Rocky Mountain bighorn sheep in Utah. Biennial Symposium of the Northern Wild Sheep and Goat Council 6: 5–12.

Stelfox, J. G. 1976. Range ecology of Rocky Mountain bighorn sheep in Canadian national parks. Canadian Wildlife Report Series No. 39.

Tilton, M. E., and E. E. Willard. 1982. Winter habitat selection by mountain sheep. Journal of Wildlife Management 46:359–366.

Van Dyke, W. A., A. Sands, J. Yoakum, A. Polentz, and J. Blaisdell. 1983. Wildlife habitat in managed rangelands—the Great Basin of southeastern Oregon: bighorn sheep. USDA Forest Service

General Technical Report PNW-159. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 37 pp.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893–901.

WEHAUSEN, J. D. 1983. Sierra Nevada bighorn sheep: history and population ecology. National Park Service Technical Report 12, Cooperative National Park Research Studies Unit, University of California, Davis. 243 pp.

WELLS, R. E., AND F. B. WELLES. 1961. The bighorn of Death Valley. National Parks Fauna Series No. 6. 242 pp.

WILLIAMS, G. L., K. R. RUSSELL, AND W. K. SEITZ. 1977. Pattern recognition as a tool in the ecological analysis of habitat. Pages 521–531 *in* Classification, inventory, and analysis of fish and wildlife habitat, the proceedings of a national symposium. U.S. Fish and Wildlife Service, USDI. FWS/OBS-78/76.

WILSON, J. A. J. 1983. Pattern recognition habitat evaluation models for southeastern Idaho. Unpublished master's thesis, Colorado State University, Fort Collins. 104 pp.

WILSON, L. O., J. BLAISDELL, G. WELSH, R. WEAVER, R. BRIGHAM, W. KELLY, J. YOAKUM, M. HINKS, J. TURNER, AND J. DEFORGE. 1980. Desert bighorn habitat requirements and management recommendations. Desert Bighorn Sheep Council Transactions 24: 1–7.

WOODGERD, W. 1964. Population dynamics of bighorn sheep on Wildhorse Island. Journal of Wildlife Management 28: 381–391.

Received 8 January 1991
Revised 19 June 1991
Accepted 3 July 1991

Great Basin Naturalist 51(3), 1991, pp. 226–235

OBSERVATIONS ON THE DEVELOPMENTAL BIOLOGY OF *CICINDELA ARENICOLA* RUMPP (COLEOPTERA: CICINDELIDAE)

Karen Lyn Bauer[1]

ABSTRACT.—*Cicindela arenicola* Rumpp is being considered for threatened and endangered status by the U.S. Fish and Wildlife Service. Little is known about the developmental biology of this species.

Adults of *C. arenicola* were active from April through late June and late August through early November, but generally they were not on the surface when temperatures were below 19 C or above 45 C, or when conditions were windy, cloudy, or rainy. Mating and egg-laying occurred only during the spring.

Five size classes (1-, 2-, 3-, 4-, and 5-mm diameters) of larval burrow openings were observed. Burrows of 5 mm had a mean depth of 42.23 ± 8.81 cm (1 S.D.). Larvae of *C. arenicola* were active from April through June and late September through mid-November.

Developmental times and larval size were affected by food supplementation. Nearly all food-supplemented, 1-mm, first instars molted to larger second instars of 3-mm diameter. Most nonsupplemented larvae spent several months as 2-mm second instars before growing to 3 mm in diameter. Food-supplemented larvae reached the third instar in approximately 13 months, while nonsupplemented larvae took slightly over two years to reach this stage. Development from egg to adult was estimated at two years for food-supplemented larvae and three and one-half to four years for nonsupplemented larvae.

Cattle had a significant effect on larval mortality. A high percentage (76–80%) of larval *C. arenicola* that were stepped on by cattle never reopened their burrows. Only 14% of undisturbed larvae never reopened their burrows. Approximately 15% of 150 larvae marked in 1988 reopened burrows in 1989.

Key words: tiger beetle, life cycle, food supplementation, mortality factors.

Eighty-five species of tiger beetles of the genus *Cicindela* exist in the United States (Boyd 1982). The adults of these species are more readily studied than are the larvae; thus, the majority of larvae are poorly known biologically.

One to several years are required for cicindelids to develop from egg through three larval instars to adult. Partial or complete life cycles have been worked out for only a few of the world's nearly 2000 described Cicindelidae (Willis 1967, Arnett 1963).

Most adult tiger beetles are diurnal predators that visually search for small arthropods and other prey on the surface in open, sparsely vegetated habitats. Sedentary tiger beetle larvae, which construct vertical burrows in the substrate, position themselves at the burrow entrance and wait for prey to pass within striking distance.

Cicindela arenicola Rumpp (1967), a sand-dwelling species, is being considered by the U.S. Fish and Wildlife Service for rare and endangered status. Little is known about its developmental biology. This species has been found in Idaho on the St. Anthony Sand Dunes, the Bruneau Sand Dunes, a series of sand dunes in Power County, and a few other small dunes along the Snake River Plain. The St. Anthony Sand Dune adult population is the largest (fewer than one million individuals), and the population in Power County is the second largest in the state (Anderson 1989). *C. arenicola* is the only species inhabiting the dunes in Power County.

Tiger beetle populations can be influenced by such weather conditions as temperature, moisture, wind, and cloud cover (Shelford 1908, Willis 1967, Knisley 1987, Mury Meyer 1987, Pearson and Lederhouse 1987). Availability of food is a major factor limiting tiger beetle development (Shelford 1908, Willis 1967, Palmer 1978, Palmer and Gorrick 1979, Knisley and Pearson 1984, Pearson and Knisley 1985, Knisley and Juliano 1988).

The objectives of this study were to: (1)

---

[1] Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83209

determine when the adults and larvae are active, (2) describe the developmental biology of larvae and the length of the life cycle under a supplemental food regimen and under natural conditions (no food supplementation), and (3) determine hazards and mortality factors for the populations.

MATERIALS AND METHODS

This study was conducted from May to November 1988 and April to September 1989 in the Wapi area approximately 17 miles west of American Falls, Power County, Idaho. The study site (approximately 150 m × 50 m) consists of a series of wet sand dunes surrounded by sagebrush. The sand is fine and buff colored.

This region of Idaho is classified as a cold desert with yearly precipitation averaging 10.42 inches. Droughts occurred in 1988 and 1989. Total precipitation during April through October for 1988 and 1989 was 2.53 inches and 4.34 inches, respectively, and was 40–70% of the average expected precipitation for these months (Climatological Data for Idaho 1988–1989). Average maximum ambient daytime temperatures ranged from 10–15 C in April to 30–38 C in July and August. Temperatures on the surface of the dunes at midday ranged from 19 to 60 C during the study period.

Vegetation on the dunes was sparse, prominent species being *Elymus flavescens* Scribn. and Smith (yellow wild rye), *Chrysothamnus viscidiflorus* (Hook.) Nutt. (gray rabbitbrush), *Chrysothamnus nauseosus* (Pall.) Britt. (green rabbitbrush), *Rumex venosus* Pursh (wild begonia), *Abronia mellifera* Dougl. (white sand verbena), *Oenothera pallida* Lindl. (pale evening primrose), and *Psoralea lanceolata* Pursh (lance-leaf scurf-pea). Monthly visual estimates of percentage of cover on portions of the dunes supporting larval and adult beetles were April, 4–6%; May, 7–9%; June, 15–17%; July, 15–20%; August, 11–15%; September, 9–15%; and October, 6–10%.

On 23 May 1988, 100 burrows of larval *C. arenicola* were marked by placing two surveyor's flags 8 in. apart with the larval burrow centered between them. A labeled wooden nursery tag was placed 2 in. from the burrow between the flags. Some burrows were located within a few centimeters of yellow wild rye culms, but usually they were not as close to other vegetation. Most larval burrows were located on the flattened, bowl-shaped portions of the dunes. Burrows of all diameters (1, 2, 3, 4, and 5 mm) were monitored throughout the study. The larvae in these burrows were not given supplemental food. Clear plastic, 14-ounce cups were placed over 33 larger burrows (4- and 5-mm diameter) in mid-August 1988 to capture any adult beetles as they emerged.

On 4 June 1988, 50 larval burrows, 1 mm in diameter, were marked in the same manner described above. These larvae were given supplemental food, provided as first or second instar larvae of *Tenebrio molitor* L. on the day of initial marking and every time their burrows were open (but never more often than twice each week). The *Tenebrio* larvae provided in this manner represented minimum dietary intake, as the *C. arenicola* larvae may have acquired additional prey on their own during the study period.

Twice each week during the two seasons (beginning in May 1988 and April 1989) the burrow diameters of the food-supplemented and nonsupplemented groups were measured using a draftsman's circle template. Visits to the sand dunes were made at 7- to 10-day intervals during the hot, dry periods from July through mid-August 1988.

In the 1989 season (April through July), diameters of unmarked larval burrows were measured approximately twice each week during a 30-minute traversing of the study site. Surface temperature, cloud cover, presence or absence of wind, and rainfall, if any, were noted. A visual census of the number of adult beetles present on the surface of the study site was taken.

Twelve 5-mm-diameter larval burrows were randomly chosen for depth measurements. Thin plaster was poured down each burrow and allowed to harden. The next day these burrows were excavated carefully and measured for depth.

The Bureau of Land Management has jurisdiction over the open rangeland where this study was conducted. Grazing is allowed, and it is not uncommon for cattle to roam the dunes in search of food when the available resources in the sagebrush areas dwindle. This usually occurs before the end of May. If a marked larval burrow was disturbed by cattle, it was noted.

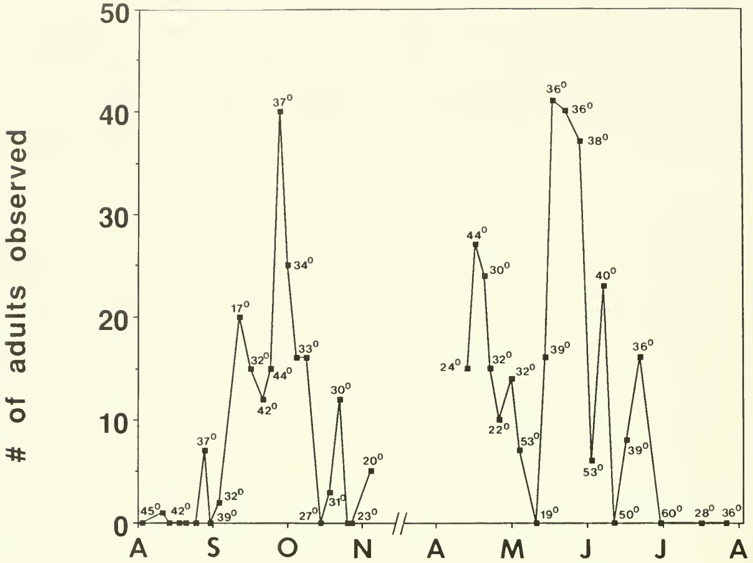


Fig. 1. Number of adult *C. arenicola* observed on study site, 2 August–5 November 1988 and 15 April–30 July 1989. Values were obtained by traversing the study site for 30 minutes twice weekly. Surface temperatures (°C) were taken at midday.

RESULTS

ADULT ACTIVITY.—Adult *C. arenicola* were active in the spring and fall on sunny, warm (19–45 C) days and also after a rain shower when the surface was moist. They burrowed beneath the sand during windy, cloudy, or cool (surface temperature below 19 C) conditions, or any combination of these. Adults were also inactive when surface temperature was above 45 C, unless clouds reduced radiant heat from the sun (Fig. 1).

Adult beetles generally appeared on the surface during the first or second week of April when they fed, mated, and laid eggs on warm, sunny days after the snow had melted. Few, if any, adults remained by the first week of July, and usually none were seen in July and August (Fig. 1). Beginning in late August or early September, fall adults emerged, with peak emergence near the end of September. Adults fed but were not observed to mate during the fall. Numbers of adults on the surface gradually diminished through October, and none were present by early November (Fig. 1). They had burrowed beneath the sand where they hibernated.

LARVAL ACTIVITY.—Five size classes (diameters) of larval burrows were observed: 1, 2, 3, 4, and 5 mm. The 5-mm burrows had a mean depth of 42.23 ± 8.81 cm (1 S.D.). The number of active larval burrows increased during April, peaked in May, and then declined through June for all size classes except the 2-mm size class, which showed its highest numbers during June (Fig. 2). Burrows were rarely open from July through mid-September. During late September through October some burrows were open, but fewer than in the spring.

A chi-square test of association (Zar 1984) was performed on the data for unmarked larval burrows, which were censused randomly in 1989. The data for 15 April, 13 May, and 14 June were used. The null hypothesis (i.e., the number of each size diameter of open larval burrows of *C. arenicola* is independent of the month in which they are measured) was rejected. A X^2 value of 146.1 was calculated

TABLE 1. Results of food supplementation of fifty 1-mm *C. arenicola* larvae monitored during June–November 1988.

	Number of times fed					
Larval growth	1	2	3	4	5	9
No change	2 (8%)	13 (87%)	4 (67%)	0	0	0
Increased one size class	0	0	0	1 (50%)	0	0
Increased two size classes	2 (8%)	2 (13%)	2 (33%)	1 (50%)	1 (100%)	1 (100%)
Never reopened	21 (84%)	0	0	0	0	0
TOTAL	25	15	6	2	1	1

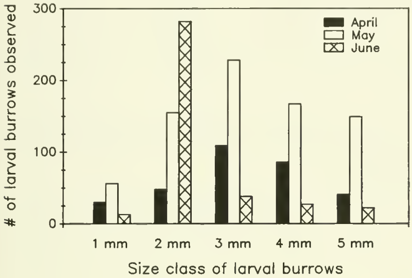


Fig. 2. Relative numbers of larval burrows of *C. arenicola* for five size classes existing at the study site, April–June 1989. Values were obtained by traversing the study site for 30 minutes twice weekly.

and compared to a table value of 15.507 at $\alpha = .05$ and 8°f.

OUTCOMES OF LARVAE.—Table 1 summarizes the results of food-supplemented larvae of *C. arenicola* during 1988. Each larva was categorized according to the number of times it accepted supplemental food and the amount of growth (increase in size class) observed. Eighty-four percent of 1-mm-diameter larvae that had one food supplement never reopened their burrows in 1988 (Table 1). Some larvae that had one to three food supplements showed no change in size class, but all larvae that received four or more food supplements increased one or two size classes (Table 1). Only three of the food-supplemented larvae showed activity in 1989. Of these three, two that received one or two supplemental feedings showed no increase in size, and one larva that received three supplemental feedings increased from the 3-mm to the 4-mm size class.

Tables 2 and 3 summarize the results of nonsupplemented larvae of *C. arenicola*. Each larva was categorized according to its size class and the amount of growth (increase in size class) observed. Larvae of 1-mm diameter showed no change or did not reopen their burrows after initial marking (Table 2). No 1-mm larvae reappeared in 1989 (Table 3). During 1988, 23 of 100 nonsupplemented larvae never reopened their burrows, 33 showed no change in size class, 26 increased one size class, 7 increased two size classes, and 1 emerged as an adult. Also during 1988, 4 nonsupplemented larvae increased three to five size classes, and 6 showed a decrease in size class (Table 2). Occasionally, a few larval burrows had irregularly shaped entrances measuring 6–7 mm. Some returned to their former size in a few days. During 1989, 18 of the 100 nonsupplemented larvae marked in 1988 were active (burrows open); 2 of these larvae opened their burrows one time only, 7 showed no change in size class, 8 increased one size class, and 1 increased two size classes (Table 3).

PROPOSED LIFE CYCLES.—Life cycles of *C. arenicola* were constructed for the food-supplemented and nonsupplemented larvae (Fig. 3). The proposed life cycle of two years for food-supplemented larvae approximates the minimum time required for development, while the life cycle of three and one-half to four years for nonsupplemented larvae approximates the maximum time required for development from egg to adult.

CATTLE ACTIVITY.—Contingency tables (Tables 4 and 5) were prepared regarding the disturbance by cattle of burrows belonging to food-supplemented and nonsupplemented larvae of *C. arenicola* and the reopening of the larval burrows after disturbance. Chi-square tests of association employing Yate's correction (Zar 1984) were performed to test the null hypotheses (i.e., there is no significant association between the reopening of burrows belonging to food-supplemented [or nonsupplemented] larvae of *C. arenicola* and whether or not the burrows had been disturbed by cattle previously). The null hypotheses were rejected in both cases, indicating that disturbance by cattle had a significant effect on the

TABLE 2. Results of each size class of 100 nonsupplemented larvae of *C. arenicola* monitored during May–November 1988.

	Size class of larval burrows				
Larval growth	1 mm	2 mm	3 mm	4 mm	5 mm
No change	1 (33%)	8 (23%)	4 (14%)	20 (63%)	0
Increased one size class	0	11 (31%)	10 (34%)	5 (16%)	0
Increased two size classes	0	5 (14%)	1 (3.5%)	1 (3%)	0
Increased three to five size classes	0	3 (9%)	1 (3.5%)	0	0
Never reopened	2 (67%)	8 (23%)	9 (31%)	3 (9%)	1 (100%)
Decreased in size class	0	0	4 (14%)	2 (6%)	0
Adult emerged	0	0	0	1 (3%)	0
TOTAL	3	35	29	32	1

TABLE 3. Results of surviving, nonsupplemented larvae of *C. arenicola* from 1988 monitored during April–September 1989.

	Size class of larval burrows			
Larval growth	2 mm	3 mm	4 mm	5 mm
No change	0	1 (50%)	5 (38%)	1 (50%)
Increased one size class	0	0	8 (62%)	0
Increased two size classes	1 (100%)	0	0	0
Never reopened	0	1 (50%)	0	1 (50%)
TOTAL	1	2	13	2

TABLE 4. Summary of the reappearance of burrows of food-supplemented larvae of *C. arenicola* related to cattle disturbance.[a]

	Supplemented larvae (1 mm)		
	Disturbed	Undisturbed	Totals
Never reopened	22	3	25
Reopened	7	18	25
TOTALS	29	21	50

[a] χ^2 18.56, α .05, 1 d f.

reopening of larval burrows. Seventy-six percent of food-supplemented larvae and 80% of nonsupplemented larvae disturbed by cattle never reopened their burrows. Fourteen percent of larvae that were undisturbed by cattle never reopened their burrows independent of whether larvae were food-supplemented or nonsupplemented (Tables 4 and 5).

It should be noted that two of the seven food-supplemented larvae that reopened their burrows after being disturbed did not reopen their burrows after one more disturbance by cattle.

TABLE 5. Summary of the reappearance of burrows of nonsupplemented larvae of *C. arenicola* related to cattle disturbance.[a]

	Nonsupplemented larvae (all size classes)		
	Disturbed	Undisturbed	Totals
Never reopened	35	8	43
Reopened	9	48	57
TOTALS	44	56	100

[a] χ^2 42.81, α .05, 1 d.f.

DISCUSSION AND CONCLUSIONS

ADULT ACTIVITY.—*Cicindela arenicola* follows seasonality patterns similar to those described for *C. repanda* Dej., *C. formosa* Say, and *C. scutellaris* Say (Knisley 1979). Typically, adults that emerged during the previous fall and spent the winter hibernating appear on the surface in April and are joined in the next several weeks by spring adults, which emerge for the first time. The spring and fall adults mature sexually, mate, and lay eggs that hatch in two to three weeks. Most of the adults die by early July. Pupae that develop during late summer produce the fall adults, and these emerge in late August and are active during September and October until they dig burrows for hibernation (Fig. 1).

The early spring peak in adults for April 1989 (Fig. 1) may represent fall adults from 1988 that had emerged from hibernation. The second peak in late May probably indicates the time of emergence of spring adults from overwintered pupae. However, Shelford (1908) reports that populations of older individuals of *C. hirticollis* Say gradually died off as the new individuals emerged, so that the

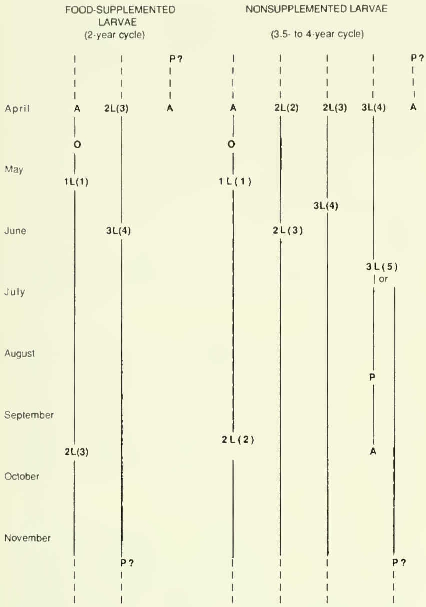


Fig. 3. Proposed life cycles for food-supplemented and nonsupplemented larvae of *C. arenicola*. (A = adult, O = oviposition, 1L = first instar, 2L = second instar, 3L = third instar, P = pupa, ---- = hibernation, ____ = active larvae.) Numbers in parentheses after instars indicate diameters (mm) of larval burrows.

presence of the younger beetles cannot be detected by population increase. This suggests that the major peak observed in May 1989 represents a majority of spring adults and fewer fall adults, many of which had mated, laid eggs, and begun to die.

The data in Figure 1 show that the majority of fall adult *C. arenicola* emerged during September. Minor peaks and sharp declines in the numbers of adult tiger beetles were probably the result of adverse weather conditions. Tiger beetles dug temporary burrows in response to very cool or very hot surface temperatures, or cloudy, rainy, or windy conditions. Willis (1967) and Pearson and Lederhouse (1987) reported similar effects of weather upon *Cicindela* species. Pearson and Lederhouse (1987), who studied the thermal ecology of 13 species of southwestern U.S. adult tiger beetles, reported a lethal (LT_{50}) maximum thoracic temperature of 47.2–48.9 C, a minimum thoracic temperature of 14.4–21.2 C, and optimum foraging temperatures of 30.2–37.2 C. Observations of surface activity recorded for adult *C. arenicola* corresponded with their results, considering that *C. arenicola* may be active at cooler surface temperatures on sunny days and at higher surface temperatures on partly cloudy days.

Cicindela arenicola was never observed to mate during the fall. Shelford (1908) reported that no female *C. hirticollis* contained eggs in the fall and that they were never seen copulating. Furthermore, hibernating species do not reach sexual maturity in autumn. Theoretically, larvae hatched from eggs laid in the fall would not be able to obtain enough food to store energy necessary to survive winter conditions. Adult tiger beetles typically reach sexual maturity in the spring and copulate on warm, sunny days.

LARVAL ACTIVITY: SIZE CLASSES.—All tiger beetles of the genus *Cicindela* that have been studied exhibit three instars, the same being presumed for *C. arenicola* (Rumpp 1967). Burrow diameter is an indication of instar because the diameter is nearly the same size as the prothorax and head width of the larva (Willis 1967, Knisley and Pearson 1984, Knisley 1987). Exact instar can be distinguished if the species is known.

Tiger beetle larvae enlarge their burrows with each molt. Shelford (1908) reported that newly molted second instar larvae of *Cicindela* possessed abdomens similar in size to late first instar larvae. Newly molted larvae have wrinkled abdominal cuticula; thus, room for growth is allowed. Palmer (1978) proposed that larvae may not molt until a certain threshold body weight is reached. Although the results were inconclusive, Palmer and Gorrick (1979) suggested that some larvae may molt at higher body weights and others at lower body weights in relation to the abundance and/or regularity of food. Molting is indicated by an increase in burrow diameter preceded by a period of plugging (Willis 1967, Knisley 1987).

Five distinct diameters of larval burrows were observed for *C. arenicola*, but this pattern probably indicates size variation within the three larval instars, not five instars for this species. Usually, periods of plugging were not observed between the 2-mm and 3-mm size classes or the 4-mm and 5-mm size classes of larval burrows. Plugging, followed by increases in burrow diameter, was observed between the 1-mm and 2–3-mm size classes, and the 3-mm and 4–5-mm size classes, indicating that molting probably occurred between these stages. Width of prothorax, by instar, for 12 species of *Cicindela* was reported by Shelford (1908). Collectively, the 12 species had pronotal width ranges of 0.7–1.75 mm ($\bar{x} \approx 1.21$ mm) for first instar larvae, 1.3–3 mm ($\bar{x} \approx 1.90$ mm) for second instars, and 1.8–5 mm ($\bar{x} \approx 3.18$ mm) for third instars. Excluding the 1.8-mm width for third instars, the pronotal widths were generally 3.5–4.5 mm for most species at the third instar stage. It can be concluded that the 1-mm size class corresponds to the first instar, the 2-mm and 3-mm size classes to second instars, and the 4-mm and 5-mm size classes to third instars for larval *C. arenicola*.

BURROW DEPTH.—Burrow depth is related to a variety of factors such as type of soil, temperature, proximity to ground water, species, and instar (Shelford 1908, Willis 1967, Knisley 1987). Larvae of sand-dwelling species usually have deeper burrows than species living in other habitats (Shelford 1908, Knisley 1987). Rumpp (1967) reported burrow depths of 15 cm for full-grown larvae of *C. arenicola*. In this study, 5-mm third instar larvae of *C. arenicola* were shown to have a burrow depth of 42.23 ± 8.81 cm. This compares favorably with the burrow depths of 15–20 cm, 30–50 cm, and 60–90 cm reported by Shelford (1908) for other sand-dwelling species. Sand becomes very dry several inches below the surface during the summer and especially during droughts. Deeper burrows allow larvae to escape desiccation and retreat to moister areas and cooler temperatures (Knisley 1987). Larvae dig deeper burrows with each successive molt. At this study site sand temperatures 30 cm or more below the surface were fairly constant (24–27 C).

NUMBERS OF LARVAL BURROWS.—Many tiger beetle larvae exhibit unimodal or bimodal (spring-fall) activity and are usually active earlier and later in the season than are the adults (Willis 1967, Knisley 1987, Mury Meyer 1987). Larval *C. arenicola* showed bimodal activity. The larval burrows appeared early in April, probably in response to warmer temperatures and surface moisture. Numbers of larval burrows increased through May, then declined during June as temperatures became much warmer, the sand dried out near the surface, and food became scarce. No larval burrows were observed in July because the larvae plugged their burrows during the hot, dry conditions. Burrow plugging has been correlated with periods of drought (Shelford 1908, Willis 1967, Knisley and Pearson 1984, Knisley 1987). Cicindelid larvae of spring-fall species may estivate during the hottest months of summer (Shelford 1908) and then reopen in the autumn when they resume feeding.

Unlike the other size classes, the 2-mm size class showed its highest numbers in June rather than May (Fig. 2). Some of these larvae may have overwintered from the previous year while others may have molted recently from the 1-mm to the 2-mm size class. Therefore, at least two generations of *C. arenicola* may be represented here.

The number of each size class of open larval burrows of *C. arenicola* is dependent upon the month in which the burrows were censused and measured, as was suggested by a chi-square test of association. Moisture (snowmelt) would be ample in April, and when combined with mild temperatures, some larvae would appear at the tops of their burrows. In May the amount of moisture might be slightly less, but with warmer temperatures, many more larvae would surface. By the end of June moisture near the soil surface is diminishing considerably and the temperatures become hot, resulting in most larvae closing their burrows, then retreating to the bottom where they spend the summer months.

OUTCOMES OF LARVAE.—Availability of food may be the limiting factor controlling tiger beetle development (Knisley and Juliano 1988). Lack of sufficient food has been reported to increase the developmental time of larval instars (Shelford 1908, Willis 1967, Knisley and Pearson 1984, Pearson and Knisley 1985, Knisley and Juliano 1988). Supplemental food decreases developmental time (Palmer 1978, Palmer and Gorrick, 1979, Knisley and Pearson 1984, Pearson and Knisley 1985, Knisley and Juliano 1988). In a comparison of food-supplemented and nonsupplemented larvae of *C. arenicola*, supplemental food decreased the time required for development, especially from first to second instar.

The high mortality shown by a majority of food-supplemented larvae that received only one feeding may have resulted from lack of sufficient food and/or desiccation, as first instar burrows are not usually very deep. If subjected to high temperatures, small larvae are unable to retreat into their burrows to much cooler depths as large instars can.

Most larvae that were fed two or three times did not show an increase in size class, suggesting that they must have obtained enough food to survive but not to store the energy to molt. Larvae fed four or more times increased one, and usually two, size classes, implying that they probably had obtained sufficient food to grow and molt to a larger size.

Willis (1967) reported that only one meal of sufficient size is required for first instar larvae to molt, and that second and third instars need several meals to accomplish the same. Evidently, for most surviving 1-mm larvae of *C. arenicola*, one small *Tenebrio* larva was not sufficient to allow molting to occur. However, if tiger beetle larvae obtained several *Tenebrio* larvae (in addition to food they captured independently), nearly all were able to skip the 2-mm size class and molt to become 3-mm larvae.

Most nonsupplemented larvae generally passed through all five size classes and did not skip sizes as their better-fed counterparts did. Mortality was substantial for first instars and somewhat less substantial for the 2- and 3-mm size classes. Desiccation may have accounted for some of the mortality seen for first instars, but lack of food was probably the major cause for most of the mortality incurred by the 1-, 2-, and 3-mm size classes.

Many larvae did not change size classes from April through October, indicating that the larvae were probably not capturing enough food to grow or molt. This trend was seen for many 4-mm larvae. The length of time spent as a third instar larva can range from several months to a few years (Shelford 1908, Willis 1967); therefore, it may not have been unusual for 4-mm (third instar) larvae of *C. arenicola* to remain the same size throughout an entire year.

Nonsupplemented larvae that increased in size usually graduated one size class. Fewer larvae increased two size classes at a time. Most of these larvae probably captured sufficient food to grow and molt, while a few of them captured enough food to skip a size class and molt at a larger size.

Occasionally, larvae showed increases of three to five size classes. This could have been the result of erosion of the burrow entrance or predators in search of food. Peculiar digging, perhaps that of small rodents, was observed where larval *C. arenicola* were located. Those larval burrows showing decreases in size could have been partially plugged when they were measured, or the original larvae might have died and new larvae hatched from eggs laid there coincidentally.

Some 4-mm larvae emerged as adults and were captured under plastic cups placed over their closed burrows in late August. Many of the 4-mm larvae that never reopened their burrows may have emerged as adults but were not caught. Most tiger beetles dig side chambers where they pupate, and the adults do not necessarily emerge along the old larval burrow (Willis 1967). The diameter of plastic cups placed over the larger burrows may not have been sufficient to capture all emerging adults.

PROPOSED LIFE CYCLES.—Rumpp (1967) predicted that the life cycle of *C. arenicola* might be similar to the two-year cycle developed by Shelford (1908) for *C. hirticollis*, a sand-dwelling species with a similar seasonality pattern. Knisley (1987) reported a two- to three-year life cycle for a population of *Cicindela marutha* Dow existing on one sand ridge and a three- to four-year life cycle for this same species on another sand ridge. His observations suggest that variability in the length of the life cycle is possible within a species.

Two years appears to be near the minimum developmental time required for food-supplemented *C. arenicola*. Food-supplemented larvae probably could not have been supplemented with food much more often than they were during the experimental period because the larvae plugged their burrows during hot, dry conditions. Nonsupplemented *C. arenicola* may take three and one-half to four years to develop from egg to adult, depending upon the abundance of food on the sand dunes. Under natural conditions, a life cycle of at least three years probably would be observed because food tends to be scarce in sand dune habitats.

The life cycle of *C. arenicola* may be variable and overlapping for several generations (i.e., second instar larvae may have reached this stage in any one of three years, making it impossible to tell which year the egg was laid that developed into a particular 2-mm or 3-mm larva). Abundance curves have been used as an indicator of the length of the life cycle for other cicindelid species (Knisley et al. 1987). Caution must be exercised in situations involving overlapping generations to reduce the possibility that more than one generation unknowingly is being monitored simultaneously. One way to do this would be to mark and monitor only first instar larvae through their full development.

CATTLE ACTIVITY.—Willis (1967) reported that cicindelids are usually absent from areas where frequent or prolonged disturbance by man or cattle occurs, although larvae are able to tolerate some amount of disturbance such as cattle walking.

Knisley et al. (1987) attributed increased vehicular traffic as a cause of a dramatic decline in populations of *C. d. dorsalis* subjected to such disturbances. Beetles were present where human activity was low and vehicles were restricted, but no beetles were present where off-road-vehicle traffic was heavy.

When cattle disturbed (stepped upon) larval burrows of *C. arenicola* once, most of the burrows never reopened. Size class and feeding status made no difference. Further disturbance caused most larvae to disappear. In contrast, significantly fewer larvae that were never disturbed by cattle never reopened their burrows. Again, size class and feeding status made no difference.

Because *C. arenicola* has a relatively long life cycle, the chance of disturbance is high in the presence of cattle. Many larvae, limited by availability of food, spend time at the tops of their burrows in order to catch prey. If disturbed at this time, the larvae are most certainly in danger of being crushed, especially because cattle sink several inches into the sand when they walk on it. Cattle were present on the dunes from the third week of May through the middle or end of September, when the BLM required them to be removed. The feeding periods of larval *C. arenicola* coincided with cattle activity on the dunes.

Suitable habitat may be reduced by frequent disturbance, and when natural mortality factors are considered, populations could be reduced to the point of extinction (Knisley et al. 1987). However, because *C. arenicola* lives in ever-changing sand dune habitats, disturbance of the surface may be important in preventing overgrowth of plants or invasion by others. Ironically, cattle impact, which appears to be so damaging to individual larval *C. arenicola*, may be providing suitable habitat for these beetles as a species.

ACKNOWLEDGMENTS

I wish to express my deep appreciation to the following individuals for their advice and expertise which made the successful completion of this project possible: Dr. R. C. Anderson for introducing me to tiger beetles and for the many hours he spent advising me through all stages of the research and writing; Dr. D. P. Streubel and Dr. D. C. Kritsky for constructive comments; Lynn Van Every for his advice and help with the graphics; my sister, Nancy Bauer, for identifying plants and for accompanying me to the study site many times over the two-year study period; and Dr. D. L. Pearson and an anonymous reviewer for constructive comments on the manuscript.

LITERATURE CITED

ANDERSON, R. C. 1989. The dunes tiger beetle. Final report for BLM Contract ID-030-CT8-005. Bureau of Land Management, Idaho Falls District. 21 pp.

ARNETT, R. H., JR. 1963. The beetles of the United States. Catholic University of America Press, Washington, D.C.

BOYD, H. P. 1982. Checklist of Cicindelidae. The tiger beetles. Plexus Publishing Company, Marlton, New Jersey.

CLIMATOLOGICAL DATA IDAHO. Jan.–Dec., 1988, Vol. 91, Nos. 1–13; Jan.–Oct., 1989, Vol. 92, Nos. 1–10. Department of Commerce, National Oceanic and Atmospheric Administration; National Environmental Satellite, Data, and Information Service; National Climatic Data Center, Asheville, North Carolina 28801.

KNISLEY, C. B. 1979. Distribution, abundance, and seasonality of tiger beetles (Cicindelidae) in the Indiana dunes region. Proceedings of the Indiana Academy of Science 88: 209–217.

______. 1987. Habitats, food resources, and natural enemies of a community of larval *Cicindela* in southeastern Arizona (Coleoptera: Cicindelidae). Canadian Journal of Zoology 65: 1191–1200.

KNISLEY, C. B., AND S. A. JULIANO. 1988. Survival, development, and size of larval tiger beetles: effects of food and water. Ecology 69: 1983–1992.

KNISLEY, C. B., J. I. LUEBKE, AND D. R. BEATTY. 1987. Natural history and population decline of the coastal tiger beetle, *Cicindela dorsalis dorsalis* Say (Coleoptera: Cicindelidae). Virginia Journal of Science 38: 293–303.

KNISLEY, C. B., AND D. L. PEARSON. 1984. Biosystematics of larval tiger beetles of the Sulphur Springs Valley, Arizona: descriptions of species and a review of larval characters for *Cicindela* (Coleoptera: Cicindelidae). Transactions of the American Entomological Society 110: 465–551.

MURY MEYER, E. J. 1987. Asymmetric resource use in two syntopic species of larval tiger beetles (Cicindelidae). Oikos 50: 167–175.

PALMER, M. K. 1978. Growth rates and survivorship of tiger beetle larvae. Cicindela 10: 49–66.

PALMER, M. K., AND M. A. GORRICK. 1979. Influence of food on development in tiger beetle larvae. Cicindela 11: 17–25.

PEARSON, D. L., AND C. B. KNISLEY. 1985. Evidence for food as a limiting resource in the life cycle of tiger beetles (Coleoptera: Cicindelidae). Oikos 45: 161–168.

PEARSON, D. L., AND R. C. LEDERHOUSE. 1987. Thermal ecology and the structure of an assemblage of adult tiger beetle species (Cicindelidae). Oikos 50: 247–255.

RUMPP, N. L. 1967. A new species of *Cicindela* from Idaho (Coleoptera: Cicindelidae). Proceedings of the California Academy of Sciences 35: 129–139.

SHELFORD, V. E. 1908. Life-histories and larval habits of the tiger beetles (Cicindelidae). Zoological Journal of the Linnaean Society 30: 157–184.

WILLIS, H. L. 1967. Bionomics and zoogeography of the tiger beetles of saline habitats in the central United States (Coleoptera: Cicindelidae). University of Kansas Science Bulletin 47: 145–313.

ZAR, J. H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Received 1 June 1990
Revised 8 April 1991
Accepted 30 April 1991

Great Basin Naturalist 51(3), 1991, pp. 236–243

TREE SIZE AND UNDERSTORY PHYTOMASS PRODUCTION IN A WESTERN JUNIPER WOODLAND

Milda R. Vaitkus[1,2] and Lee E. Eddleman[1]

ABSTRACT.—Understory phytomass production in a western juniper (*Juniperus occidentalis*) woodland was examined relative to tree size in central Oregon in 1983 and 1984. Vegetation was sampled in two zones, the canopy zone (beneath the canopy) and the intercanopy zone (the space between canopies), on two adjacent sites—a lower slope site with shallow soil and an upper slope site with deeper soil. Sampling was stratified into three tree size classes. Individual species production was significantly affected by tree size and location relative to tree canopy. Production of bottlebrush squirreltail, bluebunch wheatgrass, cheatgrass, miscellaneous annual grasses, perennial forbs, and annual forbs increased with increasing tree size. Sandberg bluegrass production was greater in the intercanopy than the canopy zone, while production of bottlebrush squirreltail, bluebunch wheatgrass, miscellaneous annual grasses, and both perennial and annual forbs was greater in the canopy zone. Production of cheatgrass was determined by the interaction of tree size and zone. Phytomass relationships were expressed to a greater degree on the upper slope site, where total production exceeded that of the lower slope site by approximately 50% the second year of the study.

Individual trees appear to exert a great influence on associated vegetation as western juniper woodlands progress from the seedling (tree establishment) phase to closed stands of mature trees. Original community dominants appear to be spatially segregated beneath tree canopies and associated with large trees, while formerly less common species, such as cheatgrass, come to dominate the entire site.

Key words: Juniperus occidentalis, *western juniper, phytomass production, understory, tree size.*

Western juniper (*Juniperus occidentalis* Hook., subsp. *occidentalis*) was historically associated with desert-grassland vegetation and primarily occurred in open stands, on plateaus, or on edges of ponderosa pine (*Pinus ponderosa*) forests (Sowder and Mowat 1958). A dramatic increase in establishment and density of western juniper in much of the Intermountain West seems to have occurred in the late 1800s and early 1900s (Burkhardt and Tisdale 1969, Adams 1975, Young and Evans 1981). Western juniper woodlands are presently concentrated in central and eastern Oregon, with extensions into northern California, northern Nevada, southwestern Idaho, and eastern Washington (Dealy et al. 1978). Expansion of western juniper into sites originally dominated by mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana*) and perennial bunchgrasses in southwestern Idaho was found to be directly related to cessation of fire (Burkhardt and Tisdale 1976). Overgrazing has also been proposed as a factor contributing to increased western juniper density (Dealy et al. 1978).

Effects of increased western juniper frequency and density on associated vegetation are poorly understood. In pinyon-juniper woodlands, increases in frequency and density of trees have been shown to reduce the quantity and diversity of associated species (Dwyer 1975). Pinyon and juniper begin to exert their influence over the understory at the stage of community development characterized by an abundance of seedlings and saplings, and a few vigorous, mature trees (Blackburn and Tueller 1970). In 60–70 years, although height of trees at this point is only double that of shrubs, understory species decline at an increasingly rapid rate. As tree density increases, the understory is yet further reduced (Blackburn and Tueller 1970, Dwyer 1975, West et al. 1979, Tausch et al. 1981, Schott and Pieper 1985). Seed reserves of primary understory species decline and species diversity decreases (Koniak and Everett 1982).

Spatial patterns of understory vegetation may also develop beneath individual woodland trees. Patterns of plant cover relative to distance from the bole have been found for singleleaf pinyon (*Pinus monophylla*), Utah juniper (*Juniperus osteosperma*) (Everett and Koniak 1981), and one-seed juniper (*Juniperus monosperma*) trees (Arnold 1964). Such patterns may vary with tree size, as found by Everett et al. (1983) in singleleaf pinyon–Utah juniper stands.

---

[1] Department of Rangeland Resources, Oregon State University, Corvallis, Oregon 97331.

[2] Present address: Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802.

Climax stands of western juniper contain trees of mixed ages, ranging from first-year seedlings to trees several hundred years old, with most individuals in an intermediate age class (Burkhardt and Tisdale 1969). Seral stands are usually composed of predominantly younger age classes with a maximum age of nearly 100 years. Personal observations, as well as data from Driscoll (1964), suggest that as western juniper stands increase in age, size, and density, understory production is reduced and species composition changes. This vegetation suppression by western juniper at particular stages of woodland development has not been closely examined.

This study was begun to determine the relationship between individual trees of various sizes (ages) and the phytomass production of associated vegetation beneath and immediately adjacent to the canopy. Specifically, we wanted to identify phytomass production patterns of associated vegetation relative to western juniper tree size and location within seral stands.

METHODS

The study area is located 8.8 km southeast of Prineville in central Oregon, on a gentle north-northwest–facing slope. Long-term precipitation in Prineville (elevation 868 m), the nearest recording station, averages 254 mm annually, 89% of which occurs from October to June.

The area is representative of the Juniper Zone described by Driscoll (1964) and is characterized by the dominance of western juniper and associated shrubby vegetation, most commonly Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), and scattered low sagebrush (*Artemisia arbuscula*). Native perennial grasses include Idaho fescue (*Festuca idahoensis*), bottlebrush squirreltail (*Sitanion hystrix*), bearded bluebunch wheatgrass (*Agropyron spicatum*), and Sandberg bluegrass (*Poa sandbergii*). Cheatgrass brome (*Bromus tectorum*) and many forbs, both annual and perennial, comprise the remainder of the herbaceous component.

The study area showed no evidence of fire in the last 100 years and had been used for much of the past decade as pasture, grazed heavily during the winter and early spring. Mixed tree size classes (Burkhardt and Tisdale 1969), continuing recruitment of western juniper seedlings, the presence of locally isolated areas of vigorous bunchgrasses, along with soil characteristics, indicated the area was at an early to mid-seral successional phase.

Study sites at two elevations were selected in this area—one at an elevation of approximately 1140 m and another at 1220 m. Precipitation on each site was measured with U.S. Forest Service rain gauges. Lower site soils were relatively shallow (330 mm), clayey, mesic Aridic Durixerolls, while upper site soils were moderately deep (740 mm), clayey-skeletal, frigid Pachic Argixerolls. The soils, vegetation, fire, and grazing history are typical of the western juniper communities on soils of basaltic origin described by Driscoll (1964). Canopy cover of western juniper, determined using the line-intercept method (Canfield 1941), was 21% on the lower site and approximately 40% on the upper site.

On each site an area representative of general woodland conditions (i.e., tree size and density) was identified and a 50 × 40-m plot arbitrarily placed within it. In each plot all trees were inventoried as to height and canopy diameter and then separated into three canopy diameter size classes—small (1–3 m), intermediate (3–5 m), and large (5–9 m), corresponding to approximate average ages (determined from core samples) of 40, 55, and 75 years, respectively. From each of these three canopy size classes, five trees without overlapping canopies were randomly selected for sampling.

During June and July in both 1983 and 1984, phytomass production in the herbaceous layer was measured. The five individual trees within each size class were used as replications. Production was determined on an individual tree basis by clipping vegetation to ground level in small plots along transects corresponding to the cardinal directions.

Each transect was established within a 90-degree quadrant radiating from the bole of the tree and extending at least 1.2 m beyond the edge of the canopy. Samples were designated into two zones: the canopy zone (from the bole outward to the edge of the canopy) and the intercanopy zone (the area beyond the edge of the crown extending into the open space between tree canopies). Because each interstitial area was of different size and configuration, the intercanopy zone was restricted to an area immediately adjacent to an individual tree's canopy. Plot number and size varied with tree size to insure sampling at least 10% of each of these zones ($n = 2$ to $n = 7$; 20 × 20-cm to 50 × 60-cm plots). Samples were dried at 100 C for 24 hours and weighed. Productivity comparisons were made on the basis of grams of dry matter per square meter.

Data was log-transformed to stabilize variance, and a split-split-plot analysis of variance was used. Main plots were years (1983, 1984) and tree size (small, intermediate, large). Subplots were zones (canopy, intercanopy), and sub-subplots were quadrants (not addressed in this paper). Where interactions were not significant, main effects means were separated using Tukey's w-procedure at $P \leq .05$ (Steel and Torrie 1980). When interactions were significant, multiple comparisons were made by computing an adjusted comparison-wide probability using the Bonferroni inequality (Miller 1986). All analyses were performed using the Statistical Analysis System (SAS Inc. 1988).

RESULTS

In 1983 and 1984 total precipitation at Prineville, Oregon, was above the 30-year average, with precipitation on the study sites even higher. On-site precipitation from October to June was 420 mm and 480 mm on the lower site and 454 mm and 494 mm on the upper site for 1983 and 1984, respectively. This compared with 235 mm for the 30-year average at Prineville during the same period.

Production on both sites showed significant between-year differences, as well as year-by-size and year-by-zone interactions (Tables 1, 2). There were no three-way (year-by-size-by-zone) interactions. Total production on the lower slope site, which showed a significant year-by-size interaction (Table 1), was 38.9 g/m^2 in 1983 and 18.3 g/m^2 in 1984. Sandberg bluegrass, bottlebrush squirreltail, cheatgrass, and annual forb production comprised the greatest part of this production on the lower slope site. Production of these individual species was significantly greater in 1983 than in 1984 (Fig. 1).

On the upper slope site, total production was 42.4 g/m^2 in 1983 and 36.2 g/m^2 in 1984 and showed no between-year differences or interactions (Table 2). Species contributing most to total production on the upper slope site were Sandberg bluegrass, Idaho fescue, and perennial and annual forbs. In contrast to the lower slope site, only miscellaneous annual grasses and annual forbs showed any year-to-year differences (Fig. 1); both had significantly greater production in 1984 than in 1983.

Other relationships on both sites were confounded by interactions between main effects (Tables 1, 2). Perennial forb and total production showed significant year-by-size interactions on the lower slope site, while cheatgrass production on the upper slope site had a significant year-by-zone interaction. Because of these interactions and between-year differences in precipitation patterns, we analyzed data by individual years to examine the main effects of tree size and zone.

Tree size had a significant effect on the phytomass production of individual species on both sites (Tables 1, 2). On the lower slope site, production of bottlebrush squirreltail (1983) and perennial forbs (both years) was significantly greater associated with large trees than with small trees (Fig. 2). On the upper slope site, production of bottlebrush squirreltail (1983), bluebunch wheatgrass (1983), cheatgrass (1983), miscellaneous annual grasses (both years), perennial forbs (both years), and annual forbs (1983) was greater associated with large than small trees (Fig. 3). These relationships were reflected in significantly greater total production associated with large than with intermediate and small trees in 1984 (data not shown).

Location relative to the tree canopy also significantly affected production on both sites (Tables 1, 2). On the lower slope site (Table 1) there were significant differences in production between canopy and intercanopy zones for Sandberg bluegrass (both years), bottlebrush squirreltail (1983), bluebunch

TABLE 1. ANOVA results of log-transformed mean phytomass production on the lower slope site.

				1983			1984		
Species	Year	Year × Size	Year × Zone	Size	Zone	Size × Zone	Size	Zone	Size × Zone
Sandberg bluegrass	*	—	—	—	**	—	—	*	—
Bottlebrush squirreltail	**	—	—	*	**	—	*	**	*
Bluebunch wheatgrass	—	—	—	—	**	—	—	**	—
Cheatgrass	**	—	—	—	**	**	—	**	**
Misc. annual grasses	—	—	—	—	—	—	—	—	—
Perennial forbs	*	**	—	**	—	—	*	—	—
Annual forbs	**	—	—	—	—	—	—	**	—
Sagebrush	—	—	—	—	—	—	—	—	—
Total	**	*	—	—	—	—	**	—	*

*$p < .05$.
**$p < .01$.

TABLE 2. ANOVA results of log-transformed mean phytomass production on the upper slope site.

				1983			1984		
Species	Year	Year × Size	Year × Zone	Size	Zone	Size × Zone	Size	Zone	Size × Zone
Sandberg bluegrass	—	—	—	—	**	—	—	**	—
Idaho fescue	—	—	—	—	—	—	—	—	—
Bottlebrush squirreltail	—	—	—	**	**	—	**	**	**
Bluebunch wheatgrass	—	—	—	**	—	—	—	—	—
Cheatgrass	—	—	**	**	**	—	**	**	**
Misc. annual grasses	**	—	—	**	—	—	**	*	—
Perennial forbs	—	—	—	**	**	—	**	**	—
Annual forbs	**	—	—	**	—	—	—	**	—
Sagebrush	—	—	—	*	—	*	—	—	—
Total	—	—	—	—	—	—	*	—	—

*$p < .05$.
**$p < .01$.

wheatgrass (both years), and annual forbs (1984). On the upper slope site (Table 2) Sandberg bluegrass (both years), bottlebrush squirreltail (1983), cheatgrass (1983), miscellaneous annual grass (1984), perennial forb (both years), and annual forb (1984) production differed significantly between zones. All species, with the exception of Sandberg bluegrass, had significantly greater production in the canopy than the intercanopy zone (Figs. 4, 5). Sandberg bluegrass production was greater in the intercanopy than in the canopy zone.

Interaction between tree size and zone affected the production of several species (Tables 1, 2). Cheatgrass production on both sites was closely tied to both tree size and zone. The interaction of size and zone was significant both years on the lower slope site and in 1984 on the upper site. On the lower slope site cheatgrass production in the canopy of large trees was greater than production associated with small and intermediate trees. On the upper slope site production of cheatgrass in both zones was greater associated with large and intermediate trees than with small trees. Bottlebrush squirreltail production also showed significant interaction between size and zone. On both sites (1984) bottlebrush squirreltail canopy production was greater associated with large and intermediate trees than with small trees. These species may have contributed to significantly greater total production in the canopy zone of large versus small and intermediate trees in 1984 on the lower slope site (data not shown). Sagebrush production on the upper slope site in 1983 also showed a significant tree size-by-zone interaction (Table 2). Production of sagebrush was greater in the canopy of large than

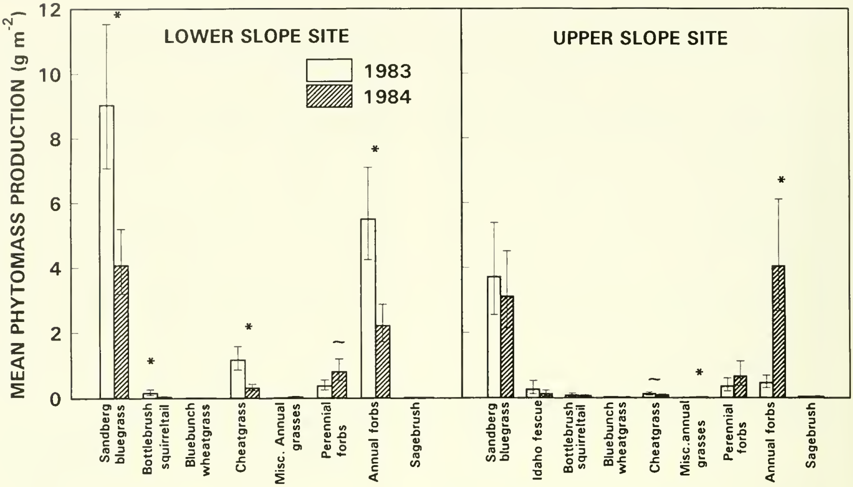


Fig. 1. Mean phytomass production (g/m^2) for each species in 1983 and 1984 on the lower slope and upper slope sites. Vertical error bars represent the 95% confidence intervals of the means. (* indicates a significant difference between years at $p < .05$, ~ indicates a significant year-by-size or year-by-zone interaction, $p < .05$.)

in small and intermediate trees, and in the intercanopy of large and intermediate than in small trees.

DISCUSSION

In this study we found that phytomass production was influenced by both tree size and zone (location relative to the tree canopy). Tree size significantly affected production of most species, especially on the upper slope site (Fig. 3). Bottlebrush squirreltail, bluebunch wheatgrass, cheatgrass, miscellaneous annual grass, and perennial and annual forb production increased as tree size increased. Sandberg bluegrass production, on the other hand, showed no relationship to tree size.

In community level studies, influences of increasing tree size have been found to negatively impact production of associated vegetation. West et al. (1979), working in singleleaf pinyon–Utah juniper communities, found that as tree size increased, understory biomass declined. Blackburn and Tueller (1970) found a reduction in the number of species present in a black sagebrush (*Artemisia nova*) community as pinyon and Utah juniper increased in size and density. Everett et al. (1983) discovered similar negative species-specific responses to tree size in singleleaf pinyon–Utah juniper communities. In these studies an increase in tree size resulted in greater competition between trees and understory vegetation, with trees outcompeting other species. Conversely, in our study large trees had a positive influence on associated vegetation. On our study site large trees appeared to act as "refuges" for most species, with greatest production associated with the largest tree size.

This importance of microsite in determining species' distribution and production was also reflected in zone relationships. Lower light levels and temperatures, higher humidity, and, possibly, greater nutrient concentrations in the canopy zone (Doescher et al. 1987) favored production of bottlebrush squirreltail, bluebunch wheatgrass, cheatgrass, miscellaneous annual grasses, and perennial forbs. Sandberg bluegrass production was always greater in the drier, warmer intercanopy zone. These patterns of individual species production relative to tree canopy are not unique to western juniper. Singleleaf pinyon (*Pinyon monophylla*) and Utah juniper (*Juniperus osteosperma*) understory plant cover (Everett and Koniak 1981) and one-seed juniper (*Juniperus monophylla*) understory

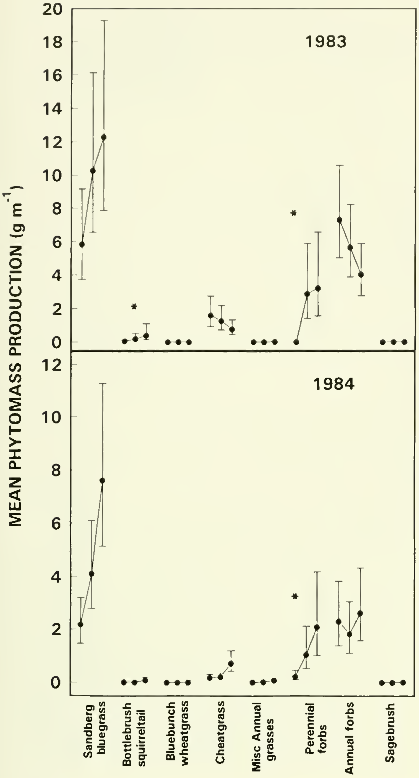


Fig. 2. Mean phytomass production (g/m^2) of the three tree size classes in 1983 and 1984 on the lower slope site. For each species, the three tick marks indicate the three tree size classes—small, intermediate, and large. Vertical error bars represent the 95% confidence intervals of the means. (* indicates a significant difference between tree size at $p < .05$, ~ indicates a significant size-by-zone interaction, $p < .05$.)

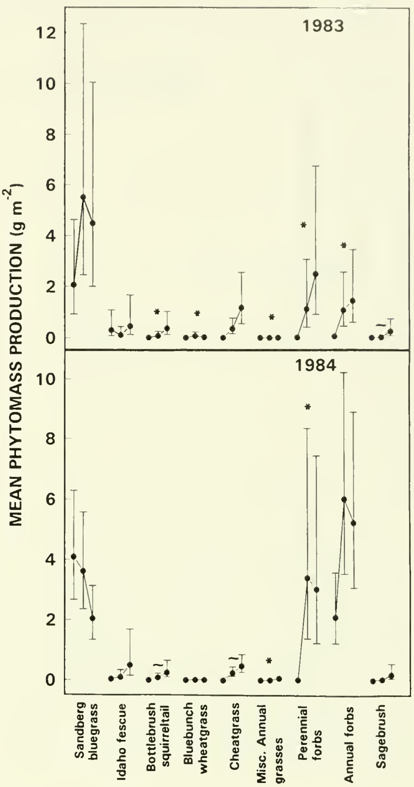


Fig. 3. Mean phytomass production (g/m^2) of the three tree size classes in 1983 and 1984 on the upper slope site. For each species, the three tick marks indicate the three tree size classes—small, intermediate, and large. Vertical error bars represent the 95% confidence intervals of the means. (* indicates a significant difference between tree size at $p < .05$, ~ indicates size-by-zone interaction, $p < .05$.)

production (Arnold 1964) were found to occur in species-specific patterns, dependent upon distance from the bole of the tree.

Composition differences in understory species between the upper and lower site may be traced to differences in elevation, the original plant community, soil depth, and, perhaps, long-term grazing. The upper site also appears to receive slightly more October through June precipitation and may be cooler during the growing season (personal observation). The shallower soils of the lower site, in combination with warmer and drier conditions, supported more squirreltail and cheatgrass. Proximity to a water source may have also resulted in heavier grazing pressure on the lower site. Idaho fescue, on the other hand, was found only on the upper slope site.

Total production tended to be greater and less variable on the upper than on the lower site. Year-to-year differences in precipitation patterns may affect species production more on the lower slope site, where soil depth precludes much storage of soil moisture.

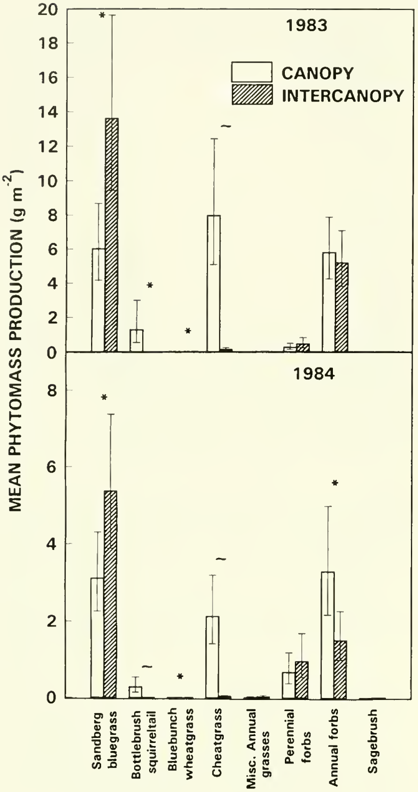


Fig. 4. Mean phytomass production (g/m^2) of the canopy and intercanopy zones in 1983 and 1984 on the lower slope site. Vertical error bars represent the 95% confidence intervals of the means. (* indicates a significant difference between zones at $p < .05$, ~ indicates a significant zone-by-size interaction, $p < .05$.)

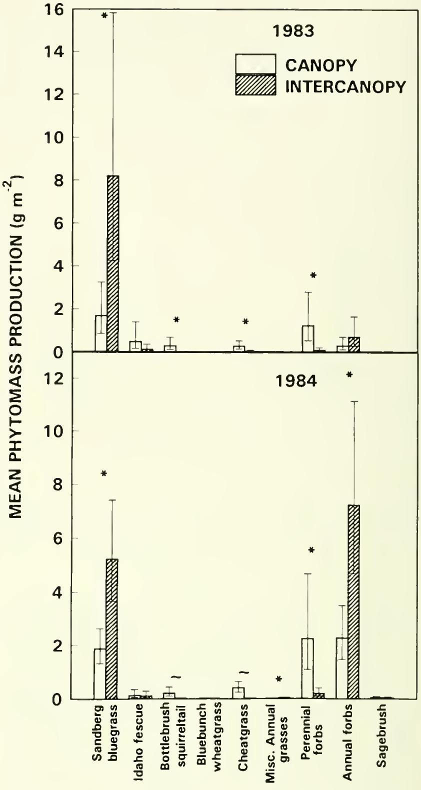


Fig. 5. Mean phytomass production (g/m^2) of the canopy and intercanopy zones in 1983 and 1984 on the upper slope site. Vertical error bars represent the 95% confidence intervals of the means. (* indicates a significant difference between zones at $p < .05$, ~ indicates a significant zone-by-size interaction, $p < .05$.)

Spatial and tree size relationships observed in this study indicate the significant role microenvironments play in species distribution and production. As individual trees increase in size (or as western juniper communities progress from tree invasion to closed stands), they exert a greater influence on associated vegetation. Original community dominants appear to become spatially segregated beneath tree canopies of large trees, while less common species, such as cheatgrass, increase across the entire site.

ACKNOWLEDGMENTS

We thank William C. Krueger, Richard F. Miller, Larry Larson, Eugene W. Schupp, and L. Katherine Kirkman for their helpful reviews of earlier versions of this manuscript. This is Technical Paper 8848 of the Oregon Agricultural Experiment Station. Preparation of this manuscript was supported by U.S. Department of Energy contract DE-AC09-76SROO-819 with the Savannah River Ecology Laboratory of the University of Georgia.

LITERATURE CITED

ADAMS, A. W. 1975. A brief history of western juniper and shrub populations in southern Oregon. Oregon State Wildlife Commission. Wildlife Research Report No. 6.

ARNOLD, J. F. 1964. Zonation of understory vegetation around a juniper tree. Journal of Range Management 17: 41–42.

BLACKBURN, W. H., AND P. T. TUELLER. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51: 841–848.

BURKHARDT, J. W., AND E. W. TISDALE. 1969. Nature and successional status of western juniper vegetation in Idaho. Journal of Range Management 22: 264–270.

_____. 1976. Causes of juniper invasion in southwestern Idaho. Ecology 57: 472–484.

CANFIELD, B. 1941. Application of the line-intercept method in sampling range vegetation. Journal of Forestry 39: 388–394.

DEALY, J. E., J. M. GEIST, AND R. S. DRISCOLL. 1978. Western juniper communities on rangelands of the Pacific Northwest. Pages 201–204 *in* Proceedings of the First International Rangeland Congress.

DOESCHER, P. S., L. E. EDDLEMAN, AND M. R. VAITKUS. 1987. Evaluation of soil nutrients, pH, and organic matter in rangelands dominated by western juniper. Northwest Science 61: 97–102.

DRISCOLL, R. S. 1964. Vegetation-soil units in the central Oregon juniper zone. USDA Forest Service Research Paper PNW-19.

DWYER, D. D. 1975. Response of livestock forage to manipulation of the pinyon-juniper ecosystem. *In:* The Pinyon-Juniper Ecosystem: A Symposium. Utah Agricultural Experiment Station, Logan, Utah.

EVERETT, R. L., AND S. KONIAK. 1981. Understory vegetation in fully stocked pinyon-juniper stands. Great Basin Naturalist 41: 467–475.

EVERETT, R. L., S. H. SHARROW, R. O. MEEUWIG. 1983. Pinyon-juniper woodland understory distribution patterns and species association. Bulletin of the Torrey Botanical Club 110: 454–463.

KONIAK, S., AND R. L. EVERETT. 1982. Seed reserves in soils of successional stages in pinyon-juniper woodlands. American Midland Naturalist 108: 295–303.

MILLER, R. G. 1986. Beyond ANOVA: basics of applied statistics. John Wiley and Sons, New York.

SAS INSTITUTE, INC. 1988. SAS/STAT user's guide: release 6.03. SAS Institute Inc., Cary, North Carolina. 1028. pp.

SCHOTT, M. R., AND R. D. PIEPER. 1985. Influence of canopy characteristics of one-seed juniper on understory grasses. Journal of Range Management 38: 328–331.

SOWDER, J. E., AND E. L. MOWAT. 1958. Silvicultural characteristics of western juniper. U.S. Forest Service PNW Forest and Range Experiment Station Silviculture Series No. 12.

STEELE, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York.

TAUSCH, R. J., N. E. WEST, AND A. A. NABI. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. Journal of Range Management 34: 259–264.

WEST, N. E., R. J. TAUSCH, AND A. A. NABI. 1979. Patterns and rates of pinyon-juniper invasion and degree of suppression of understory vegetation in the Great Basin. USDA Forest Service Range Improvement Notes, INT Region.

YOUNG, J. A., AND R. A. EVANS. 1981. Demography and fire history of a western juniper stand. Journal of Range Management 34: 501–506.

Received 8 January 1991
Revised 1 July 1991
Accepted 15 July 1991

Great Basin Naturalist 51(3), 1991, pp. 244–248

PHYSICAL CHARACTERISTICS OF BLUE GROUSE WINTER USE-TREES AND ROOST SITES

Peter J. Pekins[1], Frederick G. Lindzey[2], and James A. Gessaman[3]

Abstract.—Physical characteristics of winter use-trees and roost sites of Blue Grouse (*Dendragapus obscurus*) were studied in northeastern Utah. Blue Grouse selectively roosted in the largest Douglas-fir (*Pseudotsuga menziesii*) trees during the day and subalpine fir (*Abies lasiocarpa*) trees at night. Diurnal and nocturnal roosts were typically adjacent to tree trunks in the lower two-thirds of trees. Nocturnal roosts provided greater canopy and denser shelter than diurnal roosts. Roost site selection was consistent with occupation of favorable microhabitat, particularly at night, and foraging strategy during the day. Timber management strategies should perpetuate large trees within Douglas-fir–subalpine fir habitat in areas occupied by wintering Blue Grouse.

Key words: Abies lasiocarpa, *Blue Grouse*, Dendragapus obscurus, *Douglas-fir*, Pseudotsuga menzeisii, *roost sites, subalpine fir, winter habitat.*

Winter habitat of Blue Grouse in the intermountain region consists of snowbound open stands of conifers on moderately steep to steep upper slopes and ridgetops (Marshall 1946, Cade 1985, Stauffer and Peterson 1985). Douglas-fir is the dominant winter food and may constitute as much as 95% of the diet (Beer 1943, Stewart 1944, Marshall 1946); selectivity for Douglas-fir has been documented from use-availability measures (Cade 1985, Stauffer and Peterson 1986). Douglas-fir sites used most frequently have 45–55% tree cover and are dominated by "wolf" trees (Stauffer 1983, Cade 1985), which are uniquely large with atypical shapes and dense foliage.

Blue Grouse winter habitat relationships are usually described in terms of food habits, although other factors are likely involved. Trees used for diurnal roost sites may be chosen for a favorable microclimate in addition to food (Stauffer 1983, Cade 1985). Presumably, the selection of nocturnal use-trees by Blue Grouse is influenced by microclimatic and protective conditions. The physical characteristics of nocturnal use-trees and roost sites have not been previously described. The objective was to describe the physical characteristics of diurnal and nocturnal use-trees and associated roost sites used by Blue Grouse during winter.

Study Area

The study area is located on the Cache National Forest in the Bear River Range of the Wasatch Mountains in northeastern Utah. The primary study area is on a north-south ridge 2.5 km east of Logan Peak (USGS, Logan Peak, Utah, 7.5 min quadrangle, 1969) and encompasses approximately 700 ha. The forest is a subalpine fir/Douglas-fir mix with a shrubby undergrowth classified as the *Abies lasiocarpa* climax series–*Pseudotsuga menziesii* phase (Mauk and Henderson 1984). Topography varies from flat ridgetops to steep canyons and includes all aspects. Elevations range from 2500 to 2950 m; the regional mean January temperature is −10 C, and the mean annual precipitation is 102 cm, with 85% occurring from September through April, the majority as snow (Mauk and Henderson 1984). Snow depth on the study area ranged from approximately 2 m to 3.5 m during the winter of 1985–86. The area is characterized by strong winter temperature inversions that result in temperatures 5–10 C higher at high elevations than in valley bottoms (Wilson et al. 1975).

Methods

The point sample method (Grosenbaugh 1952) was used to inventory vegetation. A

---

[1] Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan, Utah 84322-5210. Present address: Department of Natural Resources, Pettee Hall, University of New Hampshire, Durham, New Hampshire 03824

[2] Wyoming Cooperative Research Unit, Box 3166 University Station, Laramie, Wyoming 82071.

[3] Department of Biology and Ecology Center, Utah State University, Logan, Utah 84322-5210.

40-basal-area-factor prism was used because the area was dominated by large trees. The area was inventoried along parallel transects with point samples ($n = 216$) taken at 50-m intervals along transects spaced 65 m apart. Canopy cover at each point was the average of four measurements obtained with a densitometer. Cover readings were taken parallel to the ground at waist level.

Grouse were located by ground searches and captured with a telescopic noose pole (Zwickel and Bendell 1967) when possible. Captured grouse were weighed, classified to sex and age, and fitted with a 25–30 g (<3% body weight) poncho-mounted radio transmitter (Amstrup 1980, Pekins 1988a). Diurnal use-trees and roost sites were found by locating radio-marked and unmarked Blue Grouse from December 1985 to March 1986. Any tree from which a grouse was flushed or observed was considered a use-tree, but a site was categorized as a roost only if a roosting (vs. standing) bird was observed in a nonalarmed state (e.g., crown feathers were not raised). Use-trees were marked immediately, and roost sites were marked the following day.

Nocturnal use-trees and roost sites were identified from visual sightings of radio-marked birds. The general area within a tree in which a grouse roosted was ascertained using a portable receiver and antenna. The tree was then searched with flashlights until the bird was sighted. Sites were then marked and the grouse left undisturbed.

Physical measurements of use-trees included diameter at breast height (dbh) and height. Roost site measurements included roost height, distance from tree trunk, diameter of tree trunk adjacent to the roost site, roosting branch diameter and compass direction, and percent canopy cover. Roost site height was expressed as a percentage of the total height of the tree; both heights were corrected for snow depth. Canopy cover was estimated with a densitometer. Chi-square and t tests (Steele and Torrie 1980) were used to test for differences in frequency of trees used and in physical characteristics of trees and roost sites. A level of significance was set at .05.

RESULTS

The average basal area of trees in the study area was 19.5 m^2/ha. Nearly one-third of the sample points had no trees or had trees too small to be measured with the prism. Douglas-fir, subalpine fir, and Engelmann spruce (*Picea engelmannii*) represented 51%, 47%, and 2% of the total basal area, respectively. Average canopy coverage was 44%, and an equal number of plots had canopy coverage above and below 50%; 20% had less than 10% cover since openings and forest islands were common.

We identified 270 use-trees (47 nocturnal), of which 267 were fir (Douglas or subalpine), 1 was Engelmann spruce (nocturnal), and 2 were limber pines (*Pinus flexilis*) (diurnal). Use of Douglas-fir and subalpine fir (90% and 70% of the diurnal and nocturnal use-trees, respectively) was greater than expected, based on availability ($X^2 = 127$ and 8.7, $P < .05$, respectively). For each species, average dbh of use-trees was greater ($P < .05$) than dbh of the stand average (Table 1). Ninety percent of the Douglas-fir trees used by grouse had dbh >35 cm. Douglas-fir trees used during the day were shorter than those used at night.

Physical characteristics were measured at 161 roost sites (Table 2). Diurnal and nocturnal roost sites were typically located adjacent or close to large tree trunks in the lower two-thirds of trees and were not oriented ($X^2 = 6.1$, $P > .05$) in any direction. Nocturnal subalpine roost sites had greater ($t = 6.91$, $P < .05$) canopy cover (91%) than diurnal Douglas-fir roost sites (73%), and more nocturnal than diurnal roosts were adjacent to tree trunks. Seven Douglas-fir nocturnal roosts averaged 85% canopy cover; 5 of these were 1.7 m (± 1.1) away from the tree trunk.

DISCUSSION

The study area used by Blue Grouse during winter was dominated by large Douglas-fir and subalpine fir trees in both clumped and open stands. Blue Grouse in Idaho also selected open conifer stands (50:50 ratio of conifer cover to open) dominated by islands of Douglas-fir and subalpine fir (Caswell 1954, Stauffer 1983). Wintering areas in Colorado include dense and open second growth, mature, and old-growth coniferous forests, with an average basal area (20.9 m^2/ha; Cade 1985) similar to that measured in this study.

TABLE 1. Characteristics of trees used and unused by Blue Grouse during winter, Logan, Utah, 1985–86.

	Douglas-fir (diurnal)					Subalpine-fir (nocturnal)				
	Use-tree			Stand average		Use-tree			Stand average	
	x	SE	*n*	*x*	SE	*x*	SE	*n*	*x*	SE
dbh, cm	65.0*	1.4	200	59.1	1.3	47.5*	2.7	32	38.3	1.0
Range	20.0 – 139.7					18.8 – 98.1				
Height, m	18.3*	0.4		19.4	0.4	20.9*	1.3		18.1	0.4
Range	8.7 – 30.2					8.3 – 37.0				

*Difference ($P < .05$) between use-tree and stand average.

TABLE 2. Physical characteristics of diurnal and nocturnal winter roost sites of Blue Grouse, Logan, Utah, 1985–86.

	Douglas-fir roost sites				Subalpine fir roost sites			
	Diurnal (127)[a]		Nocturnal (7)		Diurnal (5)		Nocturnal (22)	
Characteristic	*x*	SE	*x*	SE	*x*	SE	*x*	SE
Cover, %	73	2	85	4	91	1	91*	2
Southern hemisphere, %	55		43		0		36	
Lower 2/3 of tree, %	87		100		100		91	
Adjacent to trunk, %	70		14		80		82	
Distance to trunk, m	1.0	0.3 (38)	1.7	1.1 (5)	0.7 (1)		1.4	0.7 (4)
Adjacent trunk dbh, cm	38.5	4.2	40.5	5.8	29.1	13.3	32.5	3.2
Branch diameter, cm	8.8	0.3	8.8	1.2	4.2	1.5	4.2	0.3

[a] Sample size indicated by numbers within parentheses.

*Difference ($P < .05$) between diurnal-used Douglas-fir and nocturnal-used subalpine fir roost sites.

Douglas-fir with atypical growth patterns (larger dbh and shorter height) were selectively used by Blue Grouse as in other wintering areas at similar elevations (Caswell 1954, Stauffer 1983, Cade 1985). The diurnal use of atypical Douglas-firs likely reflects Blue Grouse foraging strategy (Cade 1985). The average dbh of Douglas-fir in our area (65.0 cm) is the largest reported; the average for other intermountain studies is about 50 cm. Subalpine fir trees were preferentially used as nocturnal roost sites in this study area. Blue Grouse in Colorado were often observed flushing to a subalpine fir at dusk after feeding in Douglas-fir or lodgepole pine (*Pinus contorta*) trees (T. E. Remington, personal communication).

The physical characteristics of roost sites we measured indicate that diurnal and nocturnal roost sites provide a favorable microclimate for Blue Grouse. The single exception was that grouse did not consistently roost on branches with a southerly orientation as previously reported (Hoffman 1961). However, 71% of diurnal roosting Blue Grouse observed on the study area were in sunlight (Pekins 1988b).

Moderation of wind speed is the most significant energy-saving characteristic of roost sites (Walsberg 1985). Wind speed is typically higher at the top of the canopy (Monteith 1973), and wind penetration is reduced as the horizontal structure of the vegetation is widened (Jones 1983). The typical diurnal roost site we identified provided a solid shelter (tree trunk) on one side with encircling, wide coniferous boughs that modify exposure to wind. A typical nocturnal roost site provided a solid shelter on one side surrounded by a dense network of small coniferous branches. Mistletoe often provided proximate dense growth at nocturnal roost sites.

Blue Grouse seldom ate subalpine fir foliage in our study area (<5% of the diet; Pekins, unpublished data), but they likely selected subalpine fir trees for nocturnal roosting because of its associated microclimate. Further, subalpine fir use-trees generally occurred in large, continuous stands, unlike the more variable locations of Douglas-fir use-trees. The roost tree location, large size, and dense growth presumably provided significant wind protection during the night. Measurements within both tree species substantiated that wind speed was consistently lower in subalpine fir (Pekins 1988b).

Bergerud and Gratson (1988) suggested that grouse roosting in conifers affords protection from avian predators (e.g., Goshawks [*Accipter gentilis*] and Great Horned Owls [*Bubo virginianus*]) and may serve as an alternative to occupying snow roosts for predator avoidance. They assume neither strategy is consistent with a thermoregulatory hypothesis. However, the energetic advantage for grouse occupying a thermoneutral environment in a snow roost is well documented (Marjakangas et al. 1984, Thompson and Fritzell 1988, Korhonen 1989). Blue Grouse undoubtedly benefit, although remaining vulnerable to avian predators (Goshawks killed several grouse in the study area), while roosting in conifers. However, a switch to subalpine fir from Douglas-firs suggests that energy conservation, not predator avoidance, is the primary determinant of nocturnal roost sites selection.

Forests occupied during winter by Blue Grouse in the intermountain region are frequently of limited commercial value and often in inaccessible areas (Stauffer 1983, Cade 1985). However, some Blue Grouse wintering areas have been cut or are potentially harvestable (e.g., Cade 1985, this study). Selection and patch cuts, which would ensure the presence of large conifers, are recommended management practices in Blue Grouse wintering areas (Cade 1985). Old-age stands at high elevations are irreplaceable within reasonable stand regeneration time. Loss of wintering habitat may severely impact local Blue Grouse populations.

ACKNOWLEDGMENTS

We thank G. McDaniel, R. Berger, and S. Phelps for field assistance. C. E. Braun and the *Great Basin Naturalist* editors greatly improved an earlier version of this manuscript. This project, supported by the Utah Division of Wildlife Resources and the U.S. Forest Service, was conducted under the auspices of the Utah Cooperative Fish and Wildlife Research Unit, Utah State University.

LITERATURE CITED

AMSTRUP, S. C. 1980. A radio-collar for game birds. Journal of Wildlife Management 44: 214–217.

BEER, J. R. 1943. Food habits of the Blue Grouse. Journal of Wildlife Management 7: 32–44.

BERGERUD, A. T., AND M. W. GRATSON. 1988. Survival and breeding strategies of grouse. Pages 473–575 *in* A. T. Bergerud and M. W. Gratson, eds., Adaptive strategies and population ecology of Northern Grouse. Vol. II. Theory and synthesis. University of Minnesota Press, Minneapolis.

CADE, B. S. 1985. Winter habitat preferences and migration patterns of Blue Grouse in Middle Park, Colorado. Unpublished master's thesis, Colorado State University, Fort Collins. 101 pp.

CASWELL, E. G. 1954. A preliminary study on the life history and ecology of the Blue Grouse in west central Idaho. Unpublished master's thesis, University of Idaho, Moscow. 105 pp.

GROSENBAUGH, L. R. 1952. Plotless timber estimates—new, fast, easy. Journal of Forestry 79: 89–92.

HOFFMAN, R. S. 1961. The quality of the winter food of Blue Grouse. Journal of Wildlife Management 25: 209–210.

JONES, H. G. 1983. Plants and microclimate. Cambridge University Press, New York. 323 pp.

KORHONEN, K. 1989. Heat loss of Willow Grouse (*Lagopus l. lagopus* L.) in a snowy environment. Journal of Thermal Biology 14: 27–31.

MARJAKANGAS, A., H. RINTAMAKI, AND R. HISSA. 1984. Thermal responses in the Capercaillie (*Tetrao urogallus*) and the Black Grouse (*Lyrurus tetrix*) roosting in the snow. Physiological Zoology 57: 99–104.

MARSHALL, W. H. 1946. Cover preferences, seasonal movements and food habits of Richardson's Grouse and Ruffed Grouse in southern Idaho. Wilson Bulletin 58: 42–52.

MAUK, R. L., AND J. A. HENDERSON. 1984. Coniferous forest habitat types of northern Utah. United States Department of Agriculture, Forest Service General Technical Report INT-170. 89 pp.

MONTEITH, J. L. 1973. Principles of environmental physics. American Elsevier Publishing Co., New York. 241 pp.

PEKINS, P. J. 1988a. Effects of poncho-mounted radios on Blue Grouse. Journal of Field Ornithology 59: 46–50.

______. 1988b. Winter ecological energetics of Blue Grouse. Unpublished doctoral dissertation, Utah State University, Logan. 143 pp.

STAUFFER, D. F. 1983. Seasonal habitat relationships of Ruffed and Blue Grouse in southeastern Idaho. Unpublished doctoral dissertation, University of Idaho, Moscow. 108 pp.

______. 1985. Ruffed and Blue Grouse habitat use in southeastern Idaho. Journal of Wildlife Management 49: 459–466.

______. 1986. Seasonal microhabitat relationships of Blue Grouse in southern Idaho. Great Basin Naturalist 46: 117–122.

STEWART, R. E. 1944. Food habits of the Blue Grouse. Condor 46: 112–120.

STEELE, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill Book Company, New York. 633 pp.

THOMPSON, F. R., III, AND E. K. FRITZELL. 1988. Ruffed Grouse winter roost site preference and influence on energy demands. Journal of Wildlife Management 52: 454–460.

WALSBERG, G. E. 1985. Physiological consequences of microhabitat selection. Pages 389–413 *in* M. L. Cody, ed., Habitat selection in birds. Academic Press, New York.

Wilson, L., M. E. Olsen, T. B. Hutching, A. R. Southard, and A. J. Erickson. 1975. The soils of Utah. Utah Agricultural Experiment Station Bulletin 492. 94 pp.

Zwickel, F. C., and J. F. Bendell. 1967. A snare for capturing Blue Grouse. Journal of Wildlife Management 31: 202–204.

Received 8 January 1991
Revised 19 June 1991
Accepted 15 July 1991

Great Basin Naturalist 51(3), 1991, pp. 249–255

HABITAT USE AND FOOD SELECTION OF SMALL MAMMALS NEAR A SAGEBRUSH/CRESTED WHEATGRASS INTERFACE IN SOUTHEASTERN IDAHO

David K. Koehler[1] and Stanley H. Anderson[2]

ABSTRACT.—Habitat use and food selection data were collected for deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*), Ord's kangaroo rats (*Dipodomys ordii*), and Townsend's ground squirrels (*Spermophilus townsendii*) near a sagebrush (*Artemisia tridentata*)/crested wheatgrass (*Agropyron cristatum*) interface in southeastern Idaho. Significantly more captures occurred in the native sagebrush habitat than in areas planted in crested wheatgrass or in disturbed sites. Crested wheatgrass, a prolific seed producer, still accounted for over 30% of the total captures. Montane voles and Townsend's ground squirrels (during periods of aboveground activity) used the crested wheatgrass habitat throughout the summer, while deer mice and Ord's kangaroo rats exhibited heavy use after seed set.

Key words: small mammals, food selection, habitat selection, deer mice, montane vole, Ord's kangaroo rat, Townsend's ground squirrel.

Research has been conducted on various aspects of the ecology of wildlife residing on and adjacent to the Subsurface Disposal Area (SDA) and one other low-level radioactive waste disposal site on the Idaho National Engineering Laboratory (INEL) in southeastern Idaho. Small mammals were the most frequently occurring wildlife (Arthur and Markham 1983), and densities on the SDA were considerably higher than in adjacent native vegetation types (Groves 1981). Crested wheatgrass planted on the SDA for soil stabilization and hydrologic benefits may provide food for small mammals. A prolific seed producer, it provides a readily available seed source for granivorous rodents in this cold-desert system (Arthur et al. 1986).

In other regions where crested wheatgrass has been planted for livestock grazing use, relative densities and species diversities of small mammals (Reynolds 1980, Reynolds and Trost 1980) were reduced. However, studies conducted on the INEL have shown that crested wheatgrass seedings are used by small mammals as food sources. Filipovich (1983) reported that deer mice (*Peromyscus maniculatus*), the most abundant rodent on these disposal areas, shifted to heavy use of grass seed when crested wheatgrass went to seed. Reynolds and Arthur (1983) told of a radiomarked deer mouse that would traverse a linear distance of approximately 250 m each evening from native sagebrush vegetation to the border of the SDA. This animal would then spend the night foraging near the SDA boundary before returning to its burrow at dawn.

This study was undertaken to evaluate the habitat use and food selection of small mammals near a sagebrush/crested wheatgrass interface on INEL. Efforts were concentrated on the four most abundant species of small mammals on the SDA, deer mice, montane voles, Ord's kangaroo rats, and Townsend's ground squirrels.

METHODS

The INEL is a nuclear energy research facility under the jurisdiction of the U.S. Department of Energy. It occupies approximately 231,000 ha of sagebrush desert on the upper Snake River Plain in southeastern Idaho. Average minimum and maximum daily temperatures in summer and winter range from 10 to 30 C, and −16 to −3 C, respectively. Average annual precipitation is approximately 22 cm (Clawson et al. 1989).

The SDA, a 36-ha portion of the Radioactive Waste Management Complex, has been used for the interment of solid, low-level radioactive waste since 1952. Mixed activation, fission, and transuranic radioactive wastes have been disposed at the SDA through use of shallow burial techniques.

---

[1] Idaho Department of Fish and Game, 1515 Lincoln Road, Idaho Falls, Idaho 83401.

[2] Wyoming Cooperative Fish and Wildlife Research Unit, Box 3166, University Station, Laramie, Wyoming 82071.

Vegetation on the SDA and its perimeter consists primarily of a seeded stand of crested wheatgrass. The native vegetation surrounding the SDA is a predominantly big sagebrush/bluebunch wheatgrass (*A. spicatum*) steppe (McBride et al. 1978). Additionally, several disturbed and unseeded areas are found around the periphery of the SDA. These areas typically support a sparse cover of Russian thistle, cheatgrass (*Bromus tectorum*), and green rabbitbrush (*Chrysothamnus viscidiflorus*) (Arthur 1982).

HABITAT USE.—A 6.24-ha (240 × 260-m) live-trapping grid was established on and adjacent to the SDA to examine habitat use patterns. One hundred eighty-two trapping stations were spaced at 20-m intervals on the 13 × 14 grid. Each trapping station consisted of two Sherman live traps baited with a mixture of rolled oats and whole wheat and containing nonabsorbent cotton for bedding.

Each trap station in the live-trapping grid was placed into one of three habitat type categories: native sagebrush/bluebunch wheatgrass steppe; crested wheatgrass; or recently disturbed but unseeded sites consisting of a sparse cover of Russian thistle, cheatgrass, and green rabbitbrush. Categorization was based on visual observation of the vegetative community in which the trap station occurred. Sixty-five (36%), 63 (35%), and 54 (30%) of the 182 trapping stations occurred in native sagebrush vegetation, crested wheatgrass, and disturbed sites, respectively.

Habitat use data were collected in June, July, and August 1984. Each trapping session consisted of seven consecutive nights of trapping during which traps were set prior to sunset and then checked twice nightly. Animals were carried halfway to the next trapping station prior to release to minimize the tendency to immediately reenter known traps (Price et al. 1984). Measures of habitat use were expressed in terms of total captures, captures per 100 trap nights, and percentage of captures occurring in each of the three habitat types.

Chi-square goodness-of-fit tests, including Yates' correction for continuity (Zar 1974), were used to test for differences between numbers of total captures observed versus expected in each of the three habitat types. Expected values were determined for each species by multiplying the total captures for that species by the percentage of the trap grid occupied by the particular habitat type. Results of the chi-square tests indicated whether habitat selection occurred or if use was determined by availability. Testing for significance was conducted at the $P < .05$ and $P < .01$ levels.

FOOD HABITS.—Diet composition and seasonal use of crested wheatgrass as a food for deer mice, montane voles, Ord's kangaroo rats, and Townsend's ground squirrels collected near a sagebrush/crested wheatgrass interface were evaluated. Four separate trapping periods were conducted during the year to correspond with different phenological stages of crested wheatgrass. These included June (vegetation lush and green), July (onset of desiccation), August (vegetation severely desiccated and seed set), and January and early March (vegetation dormant with winter conditions prevalent).

Two separate grids were trapped for food habit analysis of small mammals captured near a sagebrush/crested wheatgrass interface. The first grid consisted of two lines of traps in a 25 × 100-m configuration. Trap lines were oriented parallel to and 50 and 75 m from the sagebrush/crested wheatgrass interface in the native sagebrush habitat type. Because montane voles and Ord's kangaroo rats exhibited a high degree of fidelity to the crested wheatgrass and were not captured, the trapping scheme was modified. The second configuration consisted of a 75 × 350-m trap grid established perpendicular to the sagebrush/crested wheatgrass interface so that it overlapped both vegetation types. The grid began 100 m inside the crested wheatgrass and extended 250 m into the sagebrush. Trap stations were spaced at 25-m intervals. This modification also allowed documentation of movements across the sagebrush/crested wheatgrass interface.

Trapping procedures were identical for both grids as follows. Each trapping station consisted of two traps, one Museum Special snap trap and one Sherman live trap. Snap traps were baited with peanut butter while the live traps were either unbaited or baited with a small amount of whole wheat. The traps remained set continuously during trapping

TABLE 1. Total captures of small mammals in each of three habitat types on and adjacent to the SDA, June–August 1984. Significance of chi-square tests between observed versus expected numbers is shown. Captures per 100 trap nights in parentheses.

Habitat type and species	June	July	August	Total
CRESTED WHEATGRASS				
Dipodomys ordii	107 (6.1)	43 (2.4)	40 (2.3)	190** (3.6)
Microtus montanus	62** (3.5)	41** (2.3)	25** (1.4)	128** (2.4)
Peromyscus maniculatus	219** (12.4)	237** (13.4)	339** (19.2)	795** (15.0)
TOTAL	388* (22.0)	321 (18.1)	404* (22.9)	1113** (21.0)
DISTURBED SITES				
Dipodomys ordii	127** (8.4)	45** (3.0)	48** (3.2)	220** (4.9)
Microtus montanus	16 (1.1)	8 (0.5)	3 (0.2)	27** (0.6)
Peromyscus maniculatus	271 (17.9)	264 (17.5)	329 (21.8)	864 (19.0)
TOTAL	414 (27.4)	317 (21.0)	380 (25.2)	1111 (24.5)
NATIVE SAGEBRUSH				
Dipodomys ordii	25** (1.4)	7** (0.4)	7** (0.4)	39** (0.7)
Microtus montanus	5** (0.3)	0** (0.0)	2** (0.1)	7** (0.1)
Peromyscus maniculatus	436** (24.0)	358** (19.7)	498** (27.4)	1292** (23.7)
TOTAL	466 (25.7)	365 (20.1)	507 (27.9)	1338 (24.5)
TOTAL CAPTURES				
Dipodomys ordii	259 (5.1)	95 (1.9)	95 (1.9)	449 (2.9)
Microtus montanus	83 (1.6)	49 (1.0)	30 (0.6)	162 (1.0)
Peromyscus maniculatus	926 (18.2)	859 (16.9)	1166 (22.9)	2951 (19.3)
TOTAL	1268 (24.9)	1003 (19.8)	1291 (25.4)	3562 (23.2)

*$P < .05$.
**$P < .01$.

sessions and were checked at least each morning and evening. Rodents captured in live traps were immediately sacrificed by cervical dislocation.

Diet composition was determined by microhistological analysis of stomach contents. All analyses were conducted by the Composition Analysis Laboratory at Colorado State University (Sparks and Malechek 1968). Identification of plant and arthropod fragments was made by comparison of microscopic characteristics with reference specimens collected on the INEL. Unidentified species were classified by genus, family, or order. Stomach content composition was reported as the percent relative density (number of points where each item occurred relative to the total number of points in that sample) of plant or arthropod fragments identified in the sample.

RESULTS

Habitat Use

A total of 3898 captures of seven species of small mammals in 15,288 trap nights occurred during the summer of 1984. The four species of primary concern accounted for 3562 (91%) (Table 1). Deer mice were the most frequently captured species, accounting for 76% of the total. During the project, 747 deer mice, 106 montane voles, and 95 Ord's kangaroo rats were captured and used in habitat evaluation analyses. Only two Townsend's ground squirrels were caught because of their diurnal activity patterns.

Most animals (1138 or 38%) were caught in the native sagebrush habitat. The fewest captures (1111 or 31%) occurred in disturbed sites, while 1113 (31%) were made in crested wheatgrass (Table 1). Chi-square tests confirmed that the native sagebrush habitat type was used significantly ($P < .01$) more than disturbed sites or crested wheatgrass.

When captures per 100 trap nights were considered (Table 1), the results were different. Again, the highest relative density of small mammals, 28.2 individuals per 100 trap nights, was observed in sagebrush vegetation type. But the amount of use observed in the disturbed sites and crested wheatgrass habitat types was reversed. Disturbed sites accounted for 25.7 captures per 100 trap nights, while the crested wheatgrass had 22.5 captures per 100 trap nights.

Although crested wheatgrass had the lowest relative density of small mammals of any of the habitat types, all three types received considerable use. Several species of small mammals used this habitat type heavily throughout the summer or seasonally.

Montane voles exhibited a significant ($P <$ .01) selection for the crested wheatgrass habitat type and against both disturbed sites and native sagebrush habitat types. Seventy-nine percent of all captures of montane voles occurred in crested wheatgrass and 17% in disturbed sites. Thus, 96% of the montane vole captures occurred in habitat types created by waste management operations.

Ord's kangaroo rats used both disturbed sites and crested wheatgrass significantly ($P <$ .01) more and native sagebrush significantly ($P <$ .01) less than would be expected. Over 42% of all captures of kangaroo rats occurred in the crested wheatgrass habitat, while 49% of the captures occurred in disturbed sites. So, as with montane voles, a large percentage of all captures (91%) of kangaroo rats was recorded in habitat types resulting from alteration of the native sagebrush vegetation type.

Deer mice used the sagebrush habitat significantly ($P <$ .01) more than the disturbed and crested wheatgrass habitats. Nearly 44% of all captures of deer mice occurred in sagebrush, while disturbed sites and crested wheatgrass accounted for 29% and 27%, respectively. However, use of crested wheatgrass increased as the summer progressed, and by August more captures occurred in crested wheatgrass than in disturbed sites (Table 1).

Food Habits

Although an attempt was made to collect at least 10 individuals of each of the four small mammal species during each trapping session, it was not always possible because some animals were trap shy and some were found to have empty stomachs. There was a high degree of similarity in the food habits of animals collected from both trap grids. Therefore, data were pooled to evaluate food habits of small mammals collected near a sagebrush/crested wheatgrass interface.

DEER MICE.—Stomach contents of 72 deer mice were analyzed from August 1983 through June 1985. Crested wheatgrass appeared to be relatively unimportant as a food item except during periods after the grass had gone to seed. Lepidoptera larvae ranked as the most important item in diets of deer mice collected in June and constituted 71% of the fragments identified in the samples. Small amounts of crested wheatgrass were present in the samples collected in July. However, it ranked as the eighth most frequently consumed food item and composed less than 1% of the diet. Gramineae seed was the most important food item in July, making up 66% of the diet of deer mice.

There was a pronounced shift to the use of crested wheatgrass by deer mice in August. In this month, crested wheatgrass was found in 22 of the 29 (76%) animals collected; thus, it ranked as the most important food item. Coleoptera adults and Orthoptera ranked second and third, comprising 19 and 10%, respectively.

Ten deer mice were collected in January and 10 in March. Unidentified seed was the most important food item, comprising 96% of the food in these animals. Crested wheatgrass was not identified in any of these samples.

MONTANE VOLES.—Stomach contents of 20 voles were evaluated. Crested wheatgrass was the major food item for montane voles throughout the summer. Samples from all voles collected in June, July, and August contained crested wheatgrass.

ORD'S KANGAROO RATS.—Food habits of 25 kangaroo rats were evaluated. Eight animals were collected in June 1985, 5 in July 1984, and 12 in August 1983 and 1984. Four of the 8 (50%) kangaroo rats collected in June had been feeding on crested wheatgrass; thus, crested wheatgrass was the fourth most important food item. The three items that were eaten in higher percentages were pollen (33%), unidentified arthropods (18%), and plant parts from the family Compositae (16%).

In July all five animals collected had eaten crested wheatgrass. At this time crested wheatgrass ranked as the most important food item, making up 82% of the diet of these animals. Twelve animals were collected in August, and again crested wheatgrass was identified in every sample. It accounted for 91% of the diet in animals this month.

TOWNSEND'S GROUND SQUIRRELS.—Seasonal activity of the Townsend's ground squirrel appeared to be closely correlated to the availability of crested wheatgrass in its lush state. Eighty percent (8 of 10) of the ground squirrels trapped in June had used crested wheatgrass as a food source. Only one ground squirrel was trapped in July. Stomach contents of this individual consisted of only two items: crested wheatgrass (9%) and gramineae seed (91%).

DISCUSSION

Analysis of habitat use and food habits of small mammals around the SDA indicated that the crested wheatgrass habitat type was frequently utilized. Resident animals used crested wheatgrass as a food item, and seeds appeared to attract transients. The percentages of total captures of small mammals occurring in each of the three habitat types were as follows: native sagebrush vegetation (37%), disturbed and unseeded sites (33%), and crested wheatgrass (30%) (Table 1). These results were similar to those of Reynolds (1980) but were opposite those reported by Groves (1981), who found that crested wheatgrass received the most use followed by disturbed sites and then native sagebrush vegetation. Groves (1981) captured higher numbers of small mammals in the crested wheatgrass than in the other two habitat types. However, montane voles were at a high point in their population cycle at the time the earlier study was conducted, which probably accounts for the differences in results. Our results indicated that although crested wheatgrass had the lowest density of small mammals of any of the habitat types, it received considerable use. Several species of small mammals used this habitat type heavily either throughout the summer or seasonally.

Groves (1981) also reported that the densities he found in both the crested wheatgrass and native sagebrush habitat types were considerably higher than had been reported in the literature for similar vegetation types in other areas. This may have been due to the diversity of the area with three distinctive habitat types and the large amount of "edge," all in a rather confined area.

Montane voles were more dependent upon the crested wheatgrass habitat type than any other species captured during the study. Results of all small mammal studies conducted on the INEL have indicated montane voles were restricted almost exclusively to crested wheatgrass communities (Allred 1973, Reynolds 1980, Filipovich 1983, Groves and Keller 1983). Voles are typically herbivorous, but little has been reported on specific food habits for this species. Food habit analysis conducted during this study showed crested wheatgrass to be the dominant food item for montane voles on the INEL. All 19 animals captured during the summer months had crested wheatgrass in their stomachs.

Use of crested wheatgrass by kangaroo rats was substantial. This would be expected since kangaroo rats are heteromyids, and crested wheatgrass is such a prolific seed producer. Groves (1981) hypothesized that the enhanced seed supply provided by crested wheatgrass may have accounted for the high number of kangaroo rat captures in this habitat type. Most studies of the food habits of Ord's kangaroo rat have found that this animal is primarily herbivorous/granivorous, eating large amounts of seeds along with the succulent leaves of grasses, forbs, and shrubs, and with arthropods being infrequently consumed (Johnson 1961, Flake 1973, Best and Hoditschek 1982, Koehler 1988). Food habits of kangaroo rats captured near the sagebrush/crested wheatgrass interface we studied fit these broad guidelines. Crested wheatgrass was eaten throughout the summer, but its importance increased as the summer progressed. Crested wheatgrass made up 82% of the food intake in July and 91% in August. This shift to heavy use of crested wheatgrass corresponded to the time of seed set by this grass.

Deer mice are omnivorous, their food habits generally reflecting the local availability of food items (Johnson 1961). Other studies involving food habits of deer mice in southern and southeastern Idaho have found that these rodents rely heavily on arthropods, especially Coleoptera adults and Lepidoptera larvae (Halford 1981) in spring and early summer, followed by a shift to plant material in July and August (Johnson 1961, Filipovich 1983). Our results are consistent with these findings. Crested wheatgrass varied seasonally in importance as a food item. It was relatively unimportant in June, when deer mice consumed various arthropods, and was heavily used later in the summer. The shift to crested wheatgrass in July and August corresponded to the time of summer when the grass set seed.

Food habit studies on Townsend's ground squirrels have reported that these animals feed mostly on succulent green vegetation (Alcorn 1940, Johnson 1961), especially grasses (Johnson 1977, Smith and Johnson 1985). Both Scheffer (1941) and Johnson (1977) noted that the aboveground activity of Townsend's ground squirrels was highly correlated to the presence of succulent green vegetation. This was also noticed around the SDA. Ground squirrels were present and active early in the spring until about July, when the crested wheatgrass started to desiccate. At this time the animals would go into torpor until the following spring. Johnson (1977) reported that the primary food item of Townsend's ground squirrels on the Hanford Reservation in eastern Washington was Sandberg bluegrass (*Poa sandbergii*); in southern Idaho, cheatgrass provided most of the forage consumed (Smith and Johnson 1985). In both cases the primary food eaten by Townsend's ground squirrels was also the primary grass species on the study area. Crested wheatgrass was the most heavily used food item by ground squirrels around the SDA, making up the bulk of the diets of the ground squirrels analyzed. It was also common to observe ground squirrels feeding on crested wheatgrass, and freshly cut stems were often found in active burrow entrances.

The presence of crested wheatgrass affected small mammal community structure around the SDA by influencing which species were present and their relative densities. Montane voles, Ord's kangaroo rats, and Townsend's ground squirrels exhibit early colonization characteristics after a disturbance. These species, which are either absent or uncommon in the predominant native vegetative types, now compose a large portion of the small mammal community in the SDA environs. Other species, such as deer mice, have adapted to certain components of the introduced vegetation type, specifically the use of crested wheatgrass as a food source.

Although the crested wheatgrass habitat type was used less than either of the other two habitat types, more than 30% of the total captures of small mammals occurred there. Deer mice, Ord's kangaroo rats, and Townsend's ground squirrels used the crested wheatgrass habitat heavily seasonally. Montane voles used the habitat throughout the summer. The use of crested wheatgrass as a food source appeared to be a key element in attracting small mammals to this habitat type. Crested wheatgrass does influence the type of small mammal community and the densities of these animals. Thus, this unnatural community has an impact on the total diversity of wildlife in the area.

Acknowledgments

We thank the many individuals who assisted with data collection, including W. K. Bailey, R. E. Bennetts, D. A. Bexton, E. W. Buchner, M. K. Cox, L. A. Dimond, A. L. Dray, K. S. Flippin, C. M. Frazier, D. C. Fuchs, C. C. Gordon, S. T. Knick, R. J. Koehler, K. E. Kunkel, G. E. Menkens, Jr., R. W. Schneidervin, W. J. Suchy, J. F. Thompson, P. A. Tucker, and J. M. Vore.

The staff of the Radiological and Environmental Sciences Laboratory, INEL Site, Dr. O. D. Markham, D. K. Halford, Dr. T. D. Reynolds, and S. K. Rope assisted greatly in coordinating data collection with Site personnel. Funding was provided by the U.S. Department of Energy. The U.S. Fish and Wildlife Service and the University of Wyoming provided assistance.

We appreciate the reviews provided by Drs. R. E. Beiswenger, J. L. Dodd, K. J. Gutzwiller, G. E. Menkens, Jr., and B. Miller.

Literature Cited

Alcorn, J. R. 1940. Life history notes on the Piute ground squirrel. Journal of Mammalogy 21: 160–170.

Allred, D. M. 1973. Small mammals of the National Reactor Testing Station, Idaho. Great Basin Naturalist 33: 246–250.

Arthur, W. J., III. 1982. Radionuclide concentration in vegetation at a solid radioactive waste disposal area in southeastern Idaho. Journal of Environmental Quality 11: 394–399.

Arthur, W. J., and O. D. Markham. 1983. Ecological vectors of radionuclide transport at a solid radioactive waste disposal facility in southeastern Idaho. Pages 1–13 *in* O. D. Markham, ed., Idaho National Engineering Laboratory Radioecology and Ecology Programs 1983 Progress Report. IDO-12098. National Technical Information Service, Springfield, Virginia.

Arthur, W. J., O. D. Markham, C. R. Groves, and D. K. Halford. 1986. Radiation dose to small mammals inhabiting a solid-radioactive-waste disposal area. Journal of Applied Ecology 23: 13–26.

Best, T. L., and B. Hoditschek. 1982. Analysis of cheek pouch contents in Ord's kangaroo rat (*Dipodomys ordii*). Southwestern Naturalist 27: 117–124.

CLAWSON, K. L., G. E. START, AND N. R. RICKS, EDS. 1989. Climatography of the Idaho Engineering Laboratory. U.S. Department of Commerce NOAA, Idaho Falls, Idaho. 154 pp.

FILIPOVICH, M. A. 1983. Small mammal density, movement, and food habits on the SL-1 radioactive-waste disposal area, Idaho National Engineering Laboratory. Unpublished master's thesis, Idaho State University, Pocatello.

FLAKE, L. D. 1973. Food habits of four species of rodents on a shortgrass prairie in Colorado. Journal of Mammalogy 54: 636–647.

GROVES, C. R. 1981. The ecology of small mammals on the Subsurface Disposal Area, Idaho National Engineering Laboratory Site. Unpublished master's thesis, Idaho State University, Pocatello.

GROVES, C. R., AND B. L. KELLER. 1983. Ecological characteristics of small mammals on a radioactive waste disposal area in southeastern Idaho. American Midland Naturalist 109: 253–265.

HALFORD, D. K. 1981. Repopulation and food habits of *Peromyscus maniculatus* on a burned sagebrush desert in southeastern Idaho. Northwest Science 55: 44–49.

JOHNSON, D. R. 1961. The food habits of rodents on rangelands of southern Idaho. Ecology 42: 407–410.

JOHNSON, M. K. 1977. Food of Townsend ground squirrels on the Arid Land Ecology Reserve (Washington). Great Basin Naturalist 37: 128.

KOEHLER, D. K. 1988. Small mammal movement patterns around a radioactive waste disposal area in southeastern Idaho. Unpublished master's thesis, University of Wyoming, Laramie.

MCBRIDE, R., N. R. FRENCH, A. H. DAHL, AND J. E. DETMER. 1978. Vegetation types and surface soils of the Idaho National Engineering Laboratory Site. IDO-12084. National Technical Information Service, Springfield, Virginia.

PRICE, M. V., N. M. WASER, AND T. A. BASS. 1984. Effects of moonlight on microhabitat use by desert rodents. Journal of Mammalogy 65: 353–356.

REYNOLDS, T. D. 1980. Effects of some differential land management practices on small mammal populations. Journal of Mammalogy 61: 558–561.

REYNOLDS, T. D., AND W. J. ARTHUR. 1983. Preliminary report of biological intrusion studies at the Idaho National Engineering Laboratory Subsurface Disposal Area. Pages 14–21 *in* O. D. Markham, ed., Idaho National Engineering Laboratory Radioecology and Ecology Programs 1983 Progress Report. IDO-12098. National Technical Information Service, Springfield, Virginia.

REYNOLDS, T. D., AND C. H. TROST. 1980. The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. Journal of Range Management 33: 122–125.

SCHEFFER, T. H. 1941. Ground squirrel studies in the four-rivers country, Washington. Journal of Mammalogy 22: 270–279.

SMITH, G. W., AND D. R. JOHNSON. 1985. Demography of a Townsend ground squirrel population in southwestern Idaho. Ecology 66: 171–178.

SPARKS, D. R., AND J. C. MALECHEK. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21: 264–265.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Received 7 November 1990
Revised 19 June 1991
Accepted 12 July 1991

Great Basin Naturalist 51(3), 1991, pp. 256–260

EFFECTS OF CONVICT CICHLIDS ON GROWTH AND RECRUITMENT OF WHITE RIVER SPRINGFISH

Dallas Tippie[1], James E. Deacon[1], and Chih-Hsiang Ho[2]

ABSTRACT.—Observations of changes in population density of native White River springfish (*Crenichthys baileyi*) in Pahranagat Valley led to the following hypothesis: introduced convict cichlids (*Cichlasoma nigrofasciatum*) cause reduced growth and recruitment; cover reduces the magnitude of the effect. The hypothesis was tested by establishing sympatric and allopatric groups of the two species in experimental aquaria with and without cover. Change in volume (≈ mass) and length of the two species over a three-month period in spring 1986 and 1987 was measured and analyzed using 2 × 2 factorial analyses. Convict cichlids caused reduced growth and eliminated recruitment of springfish under the experimental conditions. Cover did not influence growth but positively affected recruitment of springfish in allopatry. It is likely that a portion of the reduced springfish population densities in nature can be attributed to adverse effects from introduced cichlids.

Key words: exotic species, competition, springfish, population control.

Introduced fishes have been implicated in the decline and/or extinction of native fishes throughout the world. Numerous anecdotal accounts have documented adverse effects, but few have identified the causative mechanism (Schoenherr 1981, Taylor et al. 1984). Moyle et al. (1986) noted that introduced fishes may (1) eliminate native fishes, (2) reduce their growth and survival, (3) change their community structure, or (4) have no effect. Meffe (1985) concluded that elimination of native by exotic fishes in southwestern U.S. is frequently attributable to predation. Schoenherr (1981) demonstrated that competitive interactions with exotic species can reduce survival and produce changes in community structure. Replacement of desert pupfish (*Cyprinodon macularius*) by redbelly tilapia (*Tilapia zilli*) in an irrigation drain near the Salton Sea was attributed by Schoenherr (1985, 1988) to interference with normal behavior patterns. Bestgen and Probst (1987) proposed that reductions of native fish populations in the Southwest, heretofore attributed to interactions with introduced red shiner (*Cyprinella lutrensis*), were more likely due to habitat degradation resulting in elimination of natives from habitats which were then occupied by the alien species. Jennings and Saiki (1990) suggested that a complementary distribution between red shiner and native fishes in the San Joaquin Valley, California, may represent just the first stage in colonization by red shiner. Deacon (1988) reported that after about 20 years of maintaining a complementary distribution, red shiner suddenly expanded its range upstream and, perhaps aided by an introduced parasite (Heckmann et al. 1986), nearly replaced the indigenous woundfin (*Plagopterus argentissimus*) in the Virgin River of Utah, Arizona, and Nevada. Introduced fishes obviously interact in complex and variable ways with native species.

In Pahranagat Valley, Nevada, one population of White River springfish (*Crenichthys baileyi*) was eliminated by nonnative largemouth bass (*Micropterus salmoides*) predation; and two populations were severely depressed, apparently by interaction with convict cichlids (*Cichlasoma nigrofasciatum*), shortfin mollies (*Poecilia mexicana*), sailfin mollies (*P. latipinna*), and mosquitofish (*Gambusia affinis*) (Courtenay et al. 1985). The present study was designed to examine mechanisms that may have caused the observed population reductions. Our hypothesis was that both growth and reproduction of Hiko White River springfish (*C. b. grandis*) are depressed by interactions with convict cichlids and enhanced by cover.

---

[1] Department of Biological Sciences, University of Nevada at Las Vegas, Las Vegas, Nevada 89154

[2] Department of Mathematical Sciences, University of Nevada at Las Vegas, Las Vegas, Nevada 89154

TABLE 1. Mean volumes (ml) of springfish and cichlids at the beginning (initial) and end (final) of the experimental periods. Numbers in parentheses are one standard deviation.

	Springfish				Cichlids			
	Exp. 1		Exp. 2		Exp. 1		Exp. 2	
	Initial mean	Final mean	Initial mean	Final mean	Initial mean	Final mean	Initial mean	Final mean
Allopatric/ cover	.253	.614	.461	.761	1.79	2.77	2.09	3.37
	(.152)	(.247)	(.194)	(.223)	(.847)	(1.50)	(1.30)	(2.41)
Allopatric/ no cover	.256	.529	.453	.776	1.07	3.23	2.34	4.36
	(.113)	(.204)	(.171)	(.197)	(.540)	(1.30)	(.481)	(2.57)
Sympatric/ cover	.503	.619	.553	.749	.973	2.69	2.10	4.09
	(.154)	(.150)	(.186)	(.189)	(.569)	(1.44)	(.987)	(1.52)
Sympatric/ no cover	.340	.523	.534	.735	1.21	2.58	1.66	4.48
	(.162)	(.168)	(.210)	(.254)	(.427)	(1.18)	(.576)	(2.05)

METHODS

The following experiments were conducted in March–May 1986 (experiment 1) and 1987 (experiment 2). Springfish and cichlids were kept in separate 208-liter stock aquaria for three months in 1986 and one month in 1987 prior to introduction into experimental aquaria. Experimental fish were weighed (volume displacement), measured (total length [TL], mm), and sexed at the beginning and end of the 63-day experimental period (Table 1). Volume displacement and TL were used to minimize trauma from handling. Allopatric groups containing five pairs of springfish or five pairs of cichlids were established in each of two 76-liter aquaria with and without cover. Sympatric groups, each containing three pairs of springfish and two pairs of cichlids, were established in each of two aquaria with and without cover. Cover consisted of assorted rocks and plastic plants, all used in approximately equal amounts. Commercial "spawning grass" was placed in all aquaria to encourage spawning. Fish were fed Tetramin® Staple Food at a rate of approximately 6.0% body mass twice daily to ensure that food was not a limiting factor. All aquaria were maintained at 23–26 C. One sympatric/no cover aquarium in 1986 suffered a heater malfunction and was terminated. Biological filtration was utilized in experimental aquaria: under-gravel filtration in 1986, biological-sponge filtration in 1987. The stock aquaria were filtered with outside power filters. Seventy-five percent of the water in each aquarium was changed weekly. Observations of chasing behavior were made daily for a one-minute period per aquarium. Fin and body damage was also recorded.

A series of 2 × 2 factorial analyses (Montgomery 1984, Chapter 7) was used to examine the influence of sympatry/allopatry and cover/no cover on growth in volume (mass), TL, number of chases, and extent of fin damage for each species. Significance of differences (at 5% significance level) is summarized in ANOVA tables.

RESULTS

Data on increases in volume and TL produced the same analytical results for both springfish and cichlids; only the analyses for volume are presented (Table 2). Springfish in allopatric groups grew more rapidly than they did when cichlids were present. Cover had no significant effect, but a slight interaction between sympatry/alloptary and cover/no cover may mask the main effect of cover on growth. If so, cover has a slightly negative effect. For cichlids, higher mean growth by sympatric groups was significant, but cover did not influence growth and there was no interaction between the two factors (Table 2).

Chasing by cichlids was nearly all intraspecific and caused no detectable fin damage to springfish. Among cichlids (Table 3), the two factors, sympatry/alloptary and cover/no cover, had no significant effect on aggressive behavior as measured by chasing or fin damage. Nevertheless, cichlids in experiment 2 were significantly more aggressive than in experiment 1. During experiment 2, all springfish in one sympatric tank without cover were found dead five days before experiments were terminated. We attribute this to aggressive behavior by a nesting pair of cichlids. The dead fish were intact and were weighed,

TABLE 2. Average increase in volume (ml) of springfish and cichlids fed at 12% body weight per day for 63 days (I = increase in volume; *n* = number of fish).

	Allopatric				Sympatric			
	Cover		No cover		Cover		No cover	
	I	*n*	I	*n*	I	*n*	I	*n*
EXPERIMENT 1								
Springfish	.36	10	.27	10	.12	12	.23	12
Cichlids	1.19	10	1.80	8	1.72	8	2.37	7
EXPERIMENT 2								
Springfish	.30	10	.32	10	.20	12	.17	6
Cichlids	1.28	10	1.29	7	1.99	8	2.2	6

Analysis of variance of growth data (ml) for springfish and cichlids. Factor A is sympatry/allopatry; factor B is cover/no cover.

		Springfish		Cichlids	
Source	d.f.	MS	*F*	MS	*F*
A	1	0.0351125	17.453416**	0.9248	19.9957**
B	1	0.0000125	0.006211	0.2738	5.9200
AB	1	0.0028125	1.397515	0.0072	0.1557
Error	4	0.0020125		0.04625	
Total	7	0.0065696		0.19869	

**significant at the 5% level.

TABLE 3. Mean number of intraspecific chases by cichlids per observation period and percentage of cichlids sustaining fin damage during the experimental period (experiment 1 results from Tippie and Deacon 1987).

	Chases		Fin damage	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Sympatric, no cover	0.64	1.9	87.5	100
Allopatric, no cover	0.70	6.6	60.0	100
Sympatric, with cover	0.71	5.3	62.3	100
Allopatric, with cover	0.41	9.5	50.0	90

Analysis of variance. Factors = four combinations of treatments; block = experiments 1 and 2.

	Chases			Fin damage		
Source	d.f.	MS	*F*	d.f.	MS	*F*
Factors	3	4.6959	0.8939	3	189.5883	2.1084
Block	1	54.2882	10.3349**	1	2119.0050	23.5650**
Error	3	5.2529		3	89.9217	
Total	7	64.2370		7	2398.515	

**significant at the 5% level.

measured, and included in the analysis despite a 58- rather than a 63-day growth period.

Chasing by springfish was also more prevalent in experiment 2 (Table 4) but resulted in relatively little fin damage. Most chases were more likely attributable to mating behavior than to aggression.

Reproduction by both species was variable (Table 5). Springfish produced no young during or after the experimental periods in any tank with sympatric cichlids. In contrast, springfish eggs and/or fry were observed at some time during, or following, the experimental period in all allopatric tanks. Fry were present in one of two allopatric aquaria at termination in experiment 1, but not in experiment 2; however, 14 days after removal of experimental animals, newly hatched springfish appeared in allopatric aquaria in experiment 2.

DISCUSSION

We conclude that convict cichlids can have a significant adverse effect on growth and

TABLE 4. Mean number of intraspecific chases by springfish per observation period and percentage of springfish sustaining fin damage during the experimental period (experiment 1 data from Tippie and Deacon 1987).

	Chases		Fin damage	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Sympatric, no cover	0.32	5.4	0	0
Allopatric, no cover	0	10.8	0	20
Sympatric, with cover	0.15	4.9	0	0
Allopatric, with cover	0	7.9	0	0

Analysis of variance. Factors = four combinations of treatments; block = experiments 1 and 2.

	Chases			Fin damage		
Source	d.f.	MS	*F*	d.f.	MS	*F*
Factors	3	3.3585	0.8422	3	50	1.0
Block	1	101.7451	25.5121**	1	50	1.0
Error	3	3.9881		3	50	
Total	7	109.0917		7	150	

**significant at the 5% level.

TABLE 5. Reproduction occurring during the experimental period: # = number of tanks in that category containing eggs or fry at some time during or after the experimental period; N = number of fry surviving at termination; T = number of fry appearing following termination.

	Allopatric						Sympatric					
	Cover			No cover			Cover			No cover		
	#	N	T	#	N	T	#	N	T	#	N	T
Springfish	2	11	4	2	0	9	0	0	0	0	0	0
Cichlids	1	49	0	0	0	0	1	0	0	2	99	0

recruitment of White River springfish under the experimental conditions. It seems probable that the lack of recruitment by springfish living sympatrically with cichlids results from cichlid predation on springfish eggs and fry. Presence or absence of cover had no statistically identifiable influence on growth of either species. It did positively affect springfish recruitment, but not that of cichlids. Cichlid aggression is largely intraspecific; however, when cichlids are guarding the nest, aggression can be lethal to adult springfish. Faster growth by cichlids in sympatric experimental populations may be due to their smaller number and biomass in those tanks rather than to a salubrious interspecific relationship. Conversely, springfish grew faster in allopatric aquaria in spite of higher density.

The above conclusions help interpret conditions observed in natural populations. Introductions of convict cichlids into Ash Spring in 1965 and Crystal Spring in the 1970s were closely followed by sharp drops in their respective springfish populations (Courtenay et al. 1985). Reduced growth and recruitment might well produce that result.

More recently, however, Hiko Spring added a puzzling variation to this seemingly straightforward explanation. Following elimination of springfish by largemouth bass and subsequent disappearance of bass from the spring, springfish were reintroduced. The day successful recruitment was confirmed, a few convict cichlids were observed (Baugh et al. 1985). We predicted expansion of both populations, followed by a decline in springfish numbers. The expansion occurred, but the decline did not (Deacon, unpublished data), and we therefore suspected that additional factors might be contributing to low springfish populations at Ash and Crystal springs.

At Ash Spring, elevated ammonia and nitrite levels, apparently leading to increased susceptibility of springfish to bacterial infection from *Pseudomonas* and *Aeromonas*, are factors that may contribute to low population numbers (Taylor et al. 1990). The U.S. Bureau of Land Management, following notification of the problem, took steps to remove cattle. The result was a decrease in contaminants and an increase in densities for all fish species (Taylor et al. 1990). Springfish density nonetheless remains below levels recorded prior to introduction of cichlids and mollies (Courtenay et al. 1985).

No likely alternative explanation for low springfish populations has been identified at Crystal Spring. It would seem prudent to attempt to discover whether agricultural chemicals or other potentially toxic materials or practices are associated with manipulation of the waters for irrigation. None is apparent.

Maintenance of an abundant springfish population at Hiko Spring for three years indicates that sympatry with introduced convict cichlids, while perhaps stressful, need not invariably result in scarcity of the native species. Our results demonstrate that convict cichlids can depress growth and recruitment of springfish and, under some circumstances, may cause mortality of adults. Those may be the primary causes of low populations at Ash and Crystal springs. At Hiko Spring, however, springfish are to date maintaining essentially natural population densities despite the presence of convict cichlids, mollies, and mosquitofish.

It remains unclear why the springfish population at Hiko Spring should be responding differently from those at Ash and Crystal springs. The interaction is obviously more complex than predation on larvae or depression of growth. Any or all of the following factors may be important: (1) habitat complexity, (2) differences in resource availability, (3) escape cover for larvae, (4) selection of spawning sites, or (5) other behavioral responses developed by populations of springfish and cichlids upon becoming established in a new habitat simultaneously. Clearly, a simple predator-prey model is insufficient to explain variations in springfish population densities resulting from introductions of other species.

ACKNOWLEDGMENTS

Fran Taylor provided exceptionally competent and helpful assistance with maintenance of fish stocks in the Animal Facility at University of Nevada, Las Vegas. Walter R. Courtenay and W. L. Minckley improved the manuscript substantially with their many helpful suggestions.

LITERATURE CITED

BAUGH, T. M., J. E. DEACON, AND D. WITHERS. 1985. Conservation efforts with the Hiko White River springfish *Crenichthys baileyi grandis* (Williams and Wilde). Journal of Aquariculture and Aquatic Sciences 4: 49–53.

BESTGEN, K. R., AND D. L. PROBST. 1987. Red shiner vs. native fishes: replacement or displacement? Proceedings of the Desert Fishes Council 18(1986): 209.

COURTENAY, W. R., JR., J. E. DEACON, D. W. SADA, R. C. ALLAN, AND G. L. VINYARD. 1985. Comparative status of fishes along the course of the pluvial White River, Nevada. Southwestern Naturalist 30: 503–524.

DEACON, J. E. 1988. The endangered woundfin and water management in the Virgin River, Utah, Arizona, Nevada. Fisheries 13: 18–24.

HECKMANN, R. A., J. E. DEACON, AND P. D. GREGER. 1986. Parasites of the woundfin minnow, *Plagopterus argentissimus*, and other endemic fishes from the Virgin River, Utah. Great Basin Naturalist 46: 662–675.

JENNINGS, M. R., AND M. K. SAIKI. 1990. Establishment of red shiner, *Notropis lutrensis*, in the San Joaquin Valley, California. California Fish and Game 76: 46–57.

MEFFE, G. K. 1985. Predation and species replacement in American Southwest fishes: a case study. Southwestern Naturalist 30: 173–187.

MONTGOMERY, D. C. 1984. Design and analysis of experiments. 2d ed. John Wiley and Sons, New York.

MOYLE, P. B., H. W. LI, AND B. A. BARTON. 1986. The Frankenstein effect: impact of introduced fishes in North America. Pages 415–426 *in* R. H. Stroud, ed., Fish culture in fish management. American Fisheries Society, Bethesda, Maryland.

SCHOENHERR, A. A. 1981. The role of competition in replacement of native fishes by introduced species. Pages 173–203 *in* R. J. Naiman and D. L. Soltz, eds., Fishes in North American deserts. John Wiley and Sons, New York.

———. 1985. Replacement of *Cyprinodon macularius* by *Tilapia zilli* in an irrigation drain near the Salton Sea. Proceedings of the Desert Fishes council 13(1981): 65–66.

———. 1988. A review of the life history and status of the desert pupfish, *Cyprinodon macularius*. Bulletin of the Southern California Academy of Sciences 87: 104–134.

TAYLOR, F., L. A. GILLMAN, AND J. W. PEDRETTI. 1989. Impact of cattle on two endemic fish populations in Pahranagat Valley, Nevada. Great Basin Naturalist 49: 491–495.

TAYLOR, J. N., W. R. COURTENAY, JR., AND J. A. MCCANN. 1984. Known impacts of exotic fish introductions in the continental United States. Pages 322–373 *in* W. R. Courtenay, Jr., and J. R. Stauffer, Jr., eds., Distribution, biology and management of exotic fishes. Johns Hopkins University Press, Baltimore, Maryland.

TIPPIE, D., AND J. E. DEACON. 1987. The influence of the convict cichlid on growth and reproduction of White River springfish. Proceedings of the Desert Fishes Council 18(1986): 201–204.

Received 28 December 1990
Revised 8 May 1991
Accepted 30 May 1991

Great Basin Naturalist 51(3), 1991, pp. 261–266

NEST-SITE SELECTION BY SAGE THRASHERS IN SOUTHEASTERN IDAHO

Kenneth L. Petersen[1] and Louis B. Best[2]

Abstract.—Nest sites selected by Sage Thrashers (*Oreoscoptes montanus*) in southeastern Idaho were characterized and compared with available habitat. Microhabitats within 5 m of nests had taller and more aggregated shrubs and less bare ground than the study area in general. Big sagebrush (*Artemisia tridentata wyomingensis*) plants used for nesting were taller than average available shrubs, had greater foliage density, were more often living, and more frequently had branches and foliage within 30 cm of the ground. Nest placement was specific with respect to relative nest height and distance from the top and perimeter of the support shrub. Sage Thrashers disproportionately used easterly exposures and underused westerly exposures for their nests.

Key words: Sage Thrasher, big sagebrush, shrubsteppe, Idaho, nest-site selection.

Choice of nest sites represents habitat selection on a small spatial scale (e.g., MacKenzie et al. 1982, Stauffer and Best 1986, Bekoff et al. 1987). Availability and suitability of nest sites may govern the composition of bird communities and may structure species-habitat relationships as much as do the availability of food and other resources (Martin 1988). Presumbably, patterns of nest-site selection have evolved as a result of selective pressures that have maximized nesting success. In particular, predation (e.g., Murphy 1983, Belles-Isles and Picman 1986) and microclimate (e.g., Pleszczynska 1978, Ferguson and Siegfried 1989) have been implicated as major agents in molding nest-site selection strategies.

The Sage Thrasher (*Oreoscoptes montanus*) is a common breeding bird in sagebrush-shrubsteppe communities of the western United States (Wiens and Rotenberry 1981). Previous studies of nest-site selection by Sage Thrashers (Reynolds and Rich 1978, Rich 1978, 1980, Reynolds 1981) were limited in that only a few parameters (e.g., nest height, substrate height) were investigated. Our objective was to provide a more thorough analysis of Sage Thrasher nest-site selection, including characterization of nest-site microhabitat, nest substrates, and nest placement within substrates. Further, we measured aspects of available habitat with which to compare nest sites.

Study Area and Methods

The study area, consisting of 25 ha of sagebrush shrubsteppe on the upper Snake River plain 11 km south of Howe, Idaho, is administered by the U.S. Department of Energy as part of the Idaho National Engineering Laboratory (INEL). Vegetation is dominated by big sagebrush (*Artemisia tridentata wyomingensis*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and scattered bunchgrasses. Forbs are sparse and ephemeral, litter accumulations are scant, and much of the ground is bare. In 1980, four 6.25-ha plots (250 m × 250 m) were established and gridded throughout at 25-m intervals with steel stakes affixed with colored plastic flagging.

Data were collected during the breeding seasons of 1980–1984. Nests were located by using a rope-drag technique (Petersen and Best 1985) to flush adults from their nests. Nests also were discovered by observing adults feeding young, and many nests were found incidental to other activities. Each year several nests were discovered after being abandoned, and these were included in the sample. Nests that had deteriorated or were suspected to have been built before the current year were excluded.

Habitat characteristics of each plot were quantified in June each year by using 20 × 50-cm quadrats (Daubenmire 1959) and line intercept (Canfield 1941). Each year one to four quadrats were placed 2.5 or 5 m from each grid marker (in different locations each year); percent coverage of rabbitbrush, grasses, forbs, litter, and bare ground was estimated. Additionally, the height of all sagebrush plants included totally or partially within quadrats was recorded, and the condition of each sagebrush plant was noted as dead, 25%, 50%, 75%, or 100% living. We also qualitatively estimated density of foliage on the living portions of shrubs as low, intermediate, or high. Canopy continuity (presence or absence of gaps more than 20 cm across) of each sagebrush plant was recorded, and the profile (presence or absence of any branches or foliage within 30 cm of the ground) of sagebrush plants greater than 40 cm tall was noted.

---

[1] Department of Biology, Monmouth College, Monmouth, Illinois 61462.
[2] Department of Animal Ecology, Iowa State University, Ames, Iowa 50011.

Canopy coverage and dispersion of sagebrush were estimated by line intercept. Each year 10–25 samples were taken near grid markers on each plot, different grid markers being used each year. These samples were regularly spaced to provide an even distribution of sampling effort across the plot. For each sample we recorded line intercept of sagebrush and distance between adjacent sagebrush plants that were intercepted along a 5-m tape extending in each of the four cardinal compass directions. For each sample the coefficient of variation of intershrub distances was used as an index of dispersion; the greater the index, the more clumped the shrubs. We averaged the habitat data (exclusive of individual shrub measurements) for each grid marker and used the grid markers as observational units in statistical analyses. For individual shrub measurements (height, condition, etc.), the shrubs were the observational units.

To characterize actual nest sites, we recorded the same data for shrubs supporting a nest as for those occurring within quadrats. We also estimated canopy coverage and dispersion of sagebrush along a 5-m tape extending from the nest in each of the four cardinal compass directions. Further, we recorded the height of each sagebrush plant intercepted. From 1981 to 1984 we estimated coverage of rabbitbrush, grasses, forbs, litter, and bare ground in 20 × 50-cm quadrats placed 2.5 and 5 m from each nest in each of the four cardinal directions. To minimize the potential confounding effects of vegetation change occurring between the time of nest initiation and our measurements, we took the measurements of rabbitbrush, grasses, forbs, litter, and bare ground soon after a nest had been located. However, these measurements were not recorded for nests abandoned before being located. Data were averaged for each nest so that nests were the observational units in statistical analyses. We also recorded the following measurements: (1) height of each nest (ground to nest rim), (2) distance from the nest rim to the top of the support shrub, (3) shortest horizontal distance from the center of the nest to the perimeter of the support shrub, and (4) compass orientation of the nest relative to the center of the support shrub. We calculated relative nest height as the ratio of nest height to the height of the support shrub and expressed as a percentage.

T tests and chi-square analyses were used to compare nest-site features with those of the study area in general. For most *t* tests, variances did not differ significantly between the two groups. When variances differed, we used the t' test (Sokal and Rohlf 1969: 374–375), which relaxes the assumption of variance homogeneity. There were few significant variations among years in nest-site features used by thrashers or in habitat features on the study area. Accordingly, data were pooled for all years.

RESULTS

Nest-Site Microhabitat

Sage Thrashers chose nesting areas in which sagebrush plants were significantly taller and more clumped than on the study area in general (Table 1). Percent coverages of sagebrush, rabbitbrush, grasses, forbs, and litter within 5 m of thrasher nests were slightly greater than those on the study area in general. Although none of these patterns was significant, their cumulative effect resulted in significantly less bare ground near nests than on the rest of the study area.

Nest Substrates

All nests were located in or beneath (on the ground) sagebrush plants. Shrubs selected for nesting averaged significantly taller than those representative of the study area ($t = 15.7$, df = 5079, $p < .001$). Moreover, the range of shrub sizes used for nesting was much narrower than that of the available shrubs

TABLE 1. Habitat characteristics within 5 m of Sage Thrasher nests and on the study area in general ($\bar{x}$ ± SD).

Variable	Near nests		Study area
Sagebrush height (cm)	49 ± 12 (53)[a]	*[b]	41 ± 18 (5028)
Sagebrush dispersion[c]	86 ± 19 (53)	*	77 ± 22 (401)
Sagebrush coverage (%)	23 ± 10 (53)		22 ± 11 (401)
Rabbitbrush coverage (%)	6 ± 4 (34)		5 ± 7 (484)
Grass coverage (%)	9 ± 9 (34)		8 ± 9 (484)
Forb coverage (%)	4 ± 7 (34)		3 ± 5 (484)
Litter coverage (%)	7 ± 3 (34)		6 ± 6 (484)
Bare ground (%)	50 ± 12 (34)	*	55 ± 21 (484)

[a] Sample size.
[b] Nesting microhabitat differs from study area in general ($p < .05$, t test).
[c] Coefficient of variation of intershrub distances.

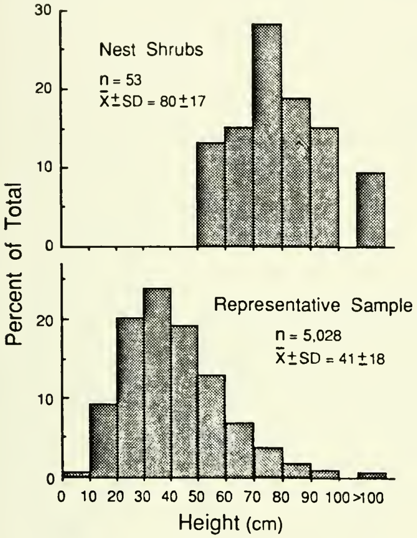


Fig. 1. Frequency distributions of heights of Sage Thrasher nest shrubs and a representative sample of sagebrush shrubs from the study area in general.

(Fig. 1). Shrubs less than 50 cm tall constituted 73% of all available shrubs; yet no shrubs in this size range were used as nest substrates. Indeed, 72% of the nests found were in or under shrubs greater than 70 cm tall; shrubs in this size range composed only 7% of all available shrubs.

Shrubs used for nesting by Sage Thrashers differed from available shrubs in several other respects. Nearly all shrubs used by thrashers were 75% or 100% living (Table 2). This differed markedly from the distribution of available shrubs among the condition classes, in which many shrubs were less than 75% living. Further, most available shrubs bearing foliage had intermediate foliage density. Although two-thirds of the nest shrubs also had intermediate foliage density, shrubs with high foliage density were used disproportionately by thrashers as nest substrates, and shrubs with low foliage density were used little. The canopy continuity of shrubs evidently did not influence shrub selection by thrashers; the frequencies with which gaps occurred in the canopies of nest shrubs and available shrubs were nearly identical. Finally, a significantly greater than expected proportion of shrubs used for nesting had branches or foliage within 30 cm of the ground.

Nest Placement Within Substrates

Thrashers placed their nests deep within or beneath shrubs (Table 3). Nest height averaged only slightly more than a third of the substrate height. Further, nests were placed horizontally relatively far from the perimeter and close to the center of the shrub. Several of these measurements are noteworthy because of their relative constancy; coefficients of variation were small for relative nest height and distances from the nest to the perimeter and the top of the shrub.

The overall pattern of Sage Thrasher nest orientations (Fig. 2) was not significantly different from a uniform distribution ($X^2 = 9.6$, 7 df, $p = .22$), but easterly (NE, E, SE) exposures were more prevalent than westerly (NW, W, SW) exposures. A comparison of all easterly orientations (combined) to all westerly orientations was significant ($X^2 = 6.1$, 1 df, $p = .02$).

DISCUSSION

Sage Thrashers were selective in their choice of nest sites. In microhabitats chosen

TABLE 2. Comparisons of Sage Thrasher nest shrubs with a representative sample of sagebrush shrubs from the study area in general. Values represent frequencies of occurrence and percentages (in parentheses) of the total.

Variable	Nest shrubs	Representative sample	χ^2	p
Condition			27.15	< .01
Dead	1 (2)	1109 (22)		
25% living	0	312 (6)		
50% living	2 (4)	617 (12)		
75% living	13 (24)	709 (14)		
100% living	37 (70)	2269 (45)		
Foliage density			5.87	.05
Low	3 (6)	515 (13)		
Intermediate	35 (67)	2762 (71)		
High	14 (27)	632 (16)		
Canopy continuity			0.01	.99
With gaps	22 (42)	2041 (41)		
Without gaps	31 (58)	2959 (59)		
Profile			4.91	.03
Full[a]	49 (92)	1875 (80)		
Not full	4 (8)	461 (20)		

[a] Branches or foliage within 30 cm of the ground.

TABLE 3. Aspects of nest placement by Sage Thrashers.

Variable[a]	$\bar{x}$	SD	CV
Nest height (cm)	30	13	43
Relative nest height (%)	37	12	33
Horizontal distance to perimeter (cm)	33	8	25
Horizontal distance to center (cm)	17	10	63
Distance to top (cm)	47	11	24

[a] $n = 53$ for all variables.

for nesting, the coverage of sagebrush seemingly was not important, but the size and spatial distribution of the shrubs were. And thrashers seemed to select areas in which total vegetation coverage was sufficient to lessen the amount of bare ground. Other studies also have documented nonrandom use of microhabitat for nest sites (e.g., MacKenzie and Sealy 1981, Petersen and Best 1985). Further, shrubs selected as nest substrates differed from the sample of shrubs representative of the study area in nearly every character that we measured.

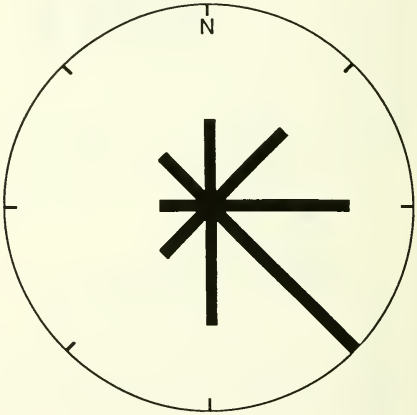


Fig. 2. Distribution of Sage Thrasher nest orientations ($n = 53$) relative to the center of the support or overhead (for ground nests) shrub. The length of each bar is proportionate to the number of nests having that orientation.

Ultimate causes of nest-site selection patterns of Sage Thrashers are unknown, but two likely selective agents are predation pressure and microclimate. For example, Sage Thrashers may place their nests in large shrubs because their nests are large and bulky (personal observation) and would be less conspicuous in large than in small shrubs. Placement of nests in living shrubs, in shrubs with high foliage density, and in shrubs with branches and foliage within 30 cm of the ground could be influenced by the need for concealment or cover from predators or weather. Nest concealment in birds is related in part to probability of predation or amelioration of microclimate (e.g., Pleszczynska 1978, Wray and Whitmore 1979, Murphy 1983, Martin and Roper 1988). The potential importance of nest obscurement and cover for thrashers is suggested also by observations of platforms of twigs in shrub canopies above some nests (Rich 1980, 1985; personal observation). Rich (1980) believed that some such canopies were old nests, but none that we observed appeared so. In one instance that we observed, twigs were placed in the shrub canopy about one week after the nest was initiated.

Aspects of nest placement within substrates (e.g., nest height, nest orientation) also have been found to be related to nesting success (e.g., Murphy 1983, Westmoreland and Best 1985) and microclimate amelioration (Horvath 1964, Rich 1978). In particular, nonrandom nest orientation typically is thought to reflect responses by birds to prevailing winds or the radiative environment (e.g., Austin 1976, Petersen and Best 1985, Ferguson and Siegfried 1989). Favoring easterly and avoiding westerly exposures for nests may reflect attempts by thrashers to maximize exposure to the morning sun, shading from the afternoon sun, or both.

It is possible, of course, that factors other than predators or microclimate accounted for the patterns we observed. For example, selection of a large shrub for nesting may denote the need for structural support for the nest. The tendency of Sage Thrashers to select microhabitats with large, clumped shrubs might simply reflect the spatial distribution of areas conducive to robust sagebrush growth. Thus, selection of a large shrub for nesting could, de facto, place the nest in an area of large, clumped sagebrush. Or, because thrashers forage primarily on the ground (personal observation), clumped shrubs perhaps provide a favorable interspersion of shrubs and openings for foraging near the nest.

Although the determinants of nest-site selection by Sage Thrashers are not known for certain, several lines of evidence suggest that thrasher nest-site selection is strongly stereotypic. First, the use of sagebrush plants as nest substrates is ubiquitous. Reynolds and Rich (1978), Rich (1978, 1980), and Reynolds (1981) also found nests only in or under big sagebrush plants. Castrale (1982) found one thrasher nest in a juniper (*Juniperus osteosperma*) tree. To our knowledge, this is the only documented instance of a Sage Thrasher nest in anything but sagebrush. Second, Sage Thrashers are specific in that their nest sites differ in many respects from the average available habitat. Third, variation in the height of shrubs chosen (coefficient of variation = 21%, compared to 44% for the representative sample of shrubs from the study area) and in several of the nest placement variables is small (Table 3). Moreover, the mean nest shrub height is similar to means reported in other studies (Reynolds and Rich 1978, Rich 1980, Reynolds 1981, Castrale 1982). Sage Thrashers are characteristic of most sagebrush-dominated rangelands in the United States (Wiens and Rotenberry 1981), and because thrashers have evolved in sagebrush habitat, the specificity of their nest-site selection should not be surprising. The patterns that we observed likely have been molded by a long history of exposure to a particular suite of selective agents.

ACKNOWLEDGMENTS

We thank Paul Sievert and Linda Erickson-Eastwood for assistance in data collection. Several technicians of the Radiological and Environmental Sciences Laboratory (RESL) of INEL also assisted in the field, and the RESL staff provided on-site transportation and lodging. We thank Terrell Rich, Kimberly A. With, and an anonymous reviewer for critiquing earlier drafts of the manuscript. This study was funded by the Office of Health and Environmental Research, U.S. Department of Energy, and is a contribution from the INEL Radioecology-Ecology Program. Funds were administered through the Iowa Cooperative Fish and Wildlife Research Unit, U.S. Fish and Wildlife Service. This is Journal Paper No. J-13723 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project No. 2468.

LITERATURE CITED

Austin, G. T. 1976. Behavioral adaptations of the Verdin to the desert. Auk 93: 245–262.

Bekoff, M., A. C. Scott, and D. A. Conner. 1987. Nonrandom nest-site selection in Evening Grosbeaks. Condor 89: 819–829.

Belles-Isles, J., and J. Picman. 1986. Nesting losses and nest site preferences in House Wrens. Condor 88: 483–486.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39: 388–394.

CASTRALE, J. S. 1982. Effects of two sagebrush control methods on nongame birds. Journal of Wildlife Management 46: 945–952.

DAUBENMIRE, R. F. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33: 43–64.

FERGUSON, J. W. H., AND W. R. SIEGFRIED. 1989. Environmental factors influencing nest-site preference in White-browed Sparrow Weavers (*Plocepasser mahali*). Condor 91: 100–107.

HORVATH, O. 1964. Seasonal differences in Rufous Hummingbird nest height and their relation to nest climate. Ecology 45: 235–241.

MACKENZIE, D. I., AND S. G. SEALY. 1981. Nest site selection in Eastern and Western Kingbirds: a multivariate approach. Condor 83: 310–321.

MACKENZIE, D. I., S. G. SEALY, AND G. D. SUTHERLAND. 1982. Nest-site characteristics of the avian community in the dune-ridge forest, Delta Marsh, Manitoba: a multivariate analysis. Canadian Journal of Zoology 60: 2212–2223.

MARTIN, T. E. 1988. Habitat and area effects on forest bird assemblages: Is nest predation an influence? Ecology 69: 74–84.

MARTIN, T. E., AND J. A. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90: 51–57.

MURPHY, M. T. 1983. Nest success and nesting habits of Eastern Kingbirds and other flycatchers. Condor 85: 208–219.

PETERSEN, K. L., AND L. B. BEST. 1985. Nest-site selection by Sage Sparrows. Condor 87: 217–221.

PLESZCZYNSKA, W. K. 1978. Microgeographic prediction of polygyny in the Lark Bunting. Science 201: 935–937.

REYNOLDS, T. D. 1981. Nesting of the Sage Thrasher, Sage Sparrow, and Brewer's Sparrow in southeastern Idaho. Condor 83: 61–64.

REYNOLDS, T. D., AND T. RICH. 1978. Reproductive ecology of the Sage Thrasher (*Oreoscoptes montanus*) on the Snake River plain in southcentral Idaho. Auk 95: 580–582.

RICH, T. 1978. Nest placement in Sage Thrashers. Wilson Bulletin 90: 303.

______. 1980. Nest placement in Sage Thrashers, Sage Sparrows, and Brewer's Sparrows. Wilson Bulletin 92: 362–368.

______. 1985. A Sage Thrasher nest with constructed shading platform. Murrelet 66: 18–19.

SOKAL, R. R., AND J. ROHLF. 1969. Biometry. W. H. Freeman, San Francisco. 776 pp.

STAUFFER, D. F., AND L. B. BEST. 1986. Nest-site characteristics of open-nesting birds in riparian habitats in Iowa. Wilson Bulletin 98: 231–242.

WESTMORELAND, D., AND L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102: 774–780.

WIENS, J. A., AND J. T. ROTENBERRY. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51: 21–41.

WRAY, T., II, AND R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. Auk 96: 802–805.

Received 8 January 1991
Revised 29 April 1991
Accepted 15 May 1991

Great Basin Naturalist 51(3), 1991, pp. 267–270

FISHES OF BLY TUNNEL, LASSEN COUNTY, CALIFORNIA

Peter B. Moyle[1], Thomas Kennedy[1], Derek Kuda[1], Laurie Martin[1], and Gerold Grant[2]

ABSTRACT.—Leon Bly Tunnel, which connects Eagle Lake to Willow Creek, was investigated to see if the water issuing from the tunnel was lake water or spring water and to check reports of its being inhabited by fish. We found that the water was similar to that of highly alkaline Eagle Lake, despite a block placed in the tunnel in 1986. Five species of fish were found in the tunnel, the same species inhabiting both Willow Creek and Eagle Lake, although the creek was much warmer and less alkaline than the lake. The fish originated from the creek. Fish in the tunnel were either not feeding or were consuming snails (*Vorticifex* sp.), the principal invertebrate present. The largest fish (35 cm SL) captured were rainbow trout (*Oncorhynchus mykiss*).

Key words: Eagle Lake, rainbow trout, Lahontan redside, fish.

Leon Bly Tunnel was constructed in 1923 to deliver water from Eagle Lake, a large natural lake on the western edge of the Great Basin, Lassen County, California (lat. 40° 37′, long. 120° 45′), to the Honey Lake Valley for irrigation. The tunnel is about 2 km long and was cut through old lava flows. The water flows from the tunnel into a ditch that joins Willow Creek, a spring-fed stream. The tunnel was abandoned as a source of irrigation water shortly after it was built (1936) because falling lake levels reduced its ability to deliver water and a landslide partially blocked the tunnel entrance (Amesbury 1971, Purdy 1988). However, water continued to flow from the tunnel, and in November 1986 the Bureau of Land Management installed a concrete plug in the tunnel in an attempt to raise the lake level (Purdy 1988). In June and July 1990 we investigated the tunnel to see (1) if the water issuing from it was lake or spring water and (2) if there were fish in it. The latter aspect was investigated because of local tales that the tunnel was full of "blind cave fish."

STUDY AREA

Eagle Lake is a large (ca 12,500 ha) terminal lake that is alkaline (pH 8.5–9.1) and very productive (Huntsinger and Maslin 1976). It contains the only population of rainbow trout (*Oncorhynchus mykiss aquilarum*) native to the Great Basin (Busak et al. 1980), as well as tui chub (*Gila bicolor*), speckled dace (*Rhinichthys osculus*), Lahontan redside (*Richardsonius egregius*), and Tahoe sucker (*Catostomus tahoensis*). Bly Tunnel begins at the lake on the eastern shore of the southernmost of the lake's three basins but can only be entered at its mouth. A steep shaft about halfway along its length was used during the 1923 excavation and is currently barred by a locked gate. The tunnel itself is 2.1 m high and 2 m wide at the base, with walls that are about half bare rock, half concrete. The water in the tunnel is 40–50 cm deep and forms riffles and pools in places where rock has fallen into the tunnel or sand and debris have accumulated on the bottom. After leaving the tunnel, the water flows 600 m through a long, shallow ditch (average depth about 30 cm) that has little cover for fish. The ditch empties into Willow Creek, which has its origins about 1 km upstream in a series of seeps and springs that coalesce in a large, wet meadow. Willow Creek, tributary to the Susan River, contains the same fish species as Eagle Lake, with the addition of Paiute sculpin (*Cottus beldingi*), although rainbow trout are very scarce and found primarily in the 1 km of stream below the mouth of the ditch. These trout probably originated from fish planted in the stream at some earlier time.

METHODS

Total alkalinity and hardness (both as mg $CaCO_3$ per L) were measured using Bausch

---

[1] Department of Wildlife and Fisheries Biology, University of California, Davis, Davis, California 95616.
[2] Department of Biological Sciences, California State University, Chico, Chico, California 95929

TABLE 1. Some characteristics of the water of Eagle Lake, Bly Tunnel, and Willow Creek, June 1990.

	Conductivity	Alkalinity[a]	Hardness[a]	Temperature (C)	Flow (m^3/min.)	Time	Date
Eagle Lake	910	440	280	18[b]	—	1015	6/29
Bly Tunnel	860	410	260	11	4.4	1530	6/19
Headwater springs	180	60	80	21	2.0	1430	6/19
Willow Creek[c]	380	380	200	21[d]	7.7[e]	1430	6/23

[a] Mg $CaCO_3$/L.

[b] Surface temperature; coldest temperature (at 14 m) was 14 C

[c] Just below convergence with ditch from tunnel

[d] The spring flows warmed to 25 C and the tunnel water to 18 C by the time they converged.

[e] Other springs contribute to flow as well as headwater springs.

and Lomb Spectrokits (titration). Conductivity was measured using a Hach portable conductivity meter. Water velocities were determined using a Marsh-McBirney Model 201 electronic flow meter. Flows (m^3/min) were approximated at each locality by measuring depths and mean water column velocities at 10 evenly spaced places on a transect across the stream and then multiplying width by mean water column velocity (m/sec) by mean depth by 60. Fishes in Willow Creek were collected with a Smith-Root Type XI electrofisher at numerous localities during 17 June–15 July 1990 as part of a detailed study of the creek's fish fauna. The tunnel fauna was sampled on 4 July 1990 between 1300 and 1500 hr. Only the first 600 m of tunnel was investigated, and at the farthest point the light from the end of the tunnel was still faintly visible. The conductivity of the tunnel water was too high for electrofishing, so fish were collected with dipnets. This proved easy to do, as they were confused by the light from our flashlights. Samples of fish from the creek and the tunnel were killed and then preserved in a 4% formaldehyde solution for dietary analysis. Diets were determined by identifying the stomach contents and estimating relative volumes of each item using the points method of Hynes (1950). Most fish were discarded after use, but voucher specimens are in the University of California, Davis, fish collection. Tunnel invertebrates were sampled with a kick screen.

RESULTS

The chemistry of the water issuing from the tunnel had a high conductivity, hardness, and total alkalinity (Table 1). All values were only slightly lower than those of Eagle Lake and much higher than those of spring water feeding Willow Creek. Temperature of the tunnel water was 11 C, colder than either the stream or lake (Table 1). At the point it flowed into the creek it had warmed to 18 C (late afternoon). The outflow of the tunnel contributed more than half the flow of Willow Creek, raising its alkalinity, hardness, and conductivity. The tunnel water also caused lower temperatures in the creek in a reach ca 500 m below the ditch entrance. However, because the stream is wide, shallow, and without riparian vegetation (due to heavy grazing), the water temperatures below this reach were typically 23–24 C by late afternoon in late June and early July.

Fish were common in the tunnel and were first noticed approximately 20 m up from the entrance. In order of abundance, the fishes collected were Lahontan redside (25), Tahoe sucker (6), speckled dace (5), rainbow trout (2), and tui chub (1), although speckled dace and Tahoe sucker may have been undersampled because of their tendency to hide in bottom debris or in crannies along the side of the tunnel. In Willow Creek the fishes present, in order of numerical abundance, were speckled dace, Lahontan redside, Tahoe sucker, tui chub, Paiute sculpin, and rainbow trout. The size classes of fish encountered in the tunnel were similar to those found in the stream, except that young-of-year fish (<30 mm SL) seemed to be absent and the two rainbow trout captured were larger than any taken from the stream. The largest trout, which was captured and released, was a hook-jawed male in spawning colors 350 mm SL. The other trout was a 184-mm-SL male. The largest fish other than trout were two 140–150-mm-SL suckers that were also captured and released. All fishes captured were similar in coloration to fish in the stream, and the

TABLE 2. Percentages of items in diets of fishes from Willow Creek and Bly Tunnel, Lassen County, California, in July 1990. A more detailed taxonomic breakdown of the gut contents is available from the senior author.

	N	SL (mm)	No. empty stomachs	Odonata	Ephemeroptera	Trichoptera	Coleoptera	Hemiptera	Diptera	Gastropoda	Misc. invertebrates	Algae/ detritus
Lahontan redside												
Tunnel	16	75	10	—	—	—	—	6	7	86	1	—
Creek	50	59	15	—	12	18	4	5	4	9	16	32
Speckled dace												
Tunnel	5	41	5	—	—	—	—	—	—	—	—	—
Creek	55	38	39	8	71	7	—	6	2	3	—	3
Tui chub												
Tunnel	1	60	1	—	—	—	—	—	—	—	—	—
Creek[a]	18	57	1	10	56	—	2	2	—	10	15	5
Tahoe sucker												
Tunnel	4	99	3	—	—	—	—	—	—	5	—	95
Creek[a]	24	70	2	12	26	12	2	—	30	2	12	2
Rainbow trout												
Tunnel	1	184	0	—	—	—	—	—	—	100	—	—
Paiute sculpin												
Creek	21	51	8	59	6	9	—	—	6	2	17	—

[a] Excludes unidentifiable material which made up >70% of gut contents.

larger redsides had traces of red on their sides (as did the creek fishes), remnants of spawning colors (Moyle 1976). All fish appeared healthy and showed no signs of starvation. The only fish observed in the ditch between the creek and the tunnel were a few small speckled dace, which we were unable to capture. Two standard minnow traps set overnight at the mouth of the tunnel failed to catch any fish, although such sets are generally successful in Willow Creek.

The guts of fishes collected from the tunnel were either empty or full of *Vorticifex (Paraphlox)* sp., a snail that was the principal aquatic invertebrate collected in the tunnel and which literally coated the bottom in places. Two redsides, however, also contained some adult insects (Table 2). Snails were relatively uncommon in the diets of Willow Creek fish, which fed primarily on aquatic insects. The only aquatic invertebrates besides snails collected in the tunnel were large annelid worms.

DISCUSSION

The highly alkaline water flowing through Bly Tunnel clearly has its source in Eagle Lake. Presumably, underground passage cools the water to 11 C. The fish, however, most likely moved up from Willow Creek, as they are roughly in the same relative abundances in the tunnel as in the creek, except for the absence of sculpins. Further evidence of this is that the rainbow trout captured were clearly wild fish (although not native to the drainage), with the fin conformations associated with wild fish. Trout in the lake are all the result of planting, and most have deformed fins from their hatchery rearing; in addition, they are planted at sizes larger (25–30 cm) than most trout in the tunnel and creek. Scales from the 184-mm trout indicated that it was 2+ years old, a fairly typical size for a stream rainbow trout (Moyle 1976). The ages and growth patterns of Lahontan redsides from the tunnel, as revealed by examination of scales, did not seem to differ from those of stream fish.

It seems likely that the fish are recent invaders of the tunnel. Presumably, they moved up earlier in the year when the water in Willow Creek was cooler and there was less of a temperature gradient. The clear water of the outflow ditch provides little shelter from bird predation, so fish are likely to persist in this area only if they move into the tunnel. We have observed Common Mergansers in the ditch, and our studies of Willow Creek indicate that predation by several species of birds is a major factor limiting fish populations (unpublished data). Although we failed to catch any fish in minnow traps set near the tunnel mouth, the presence of adult insects in two redside stomachs indicates either that individuals occasionally may venture out to feed or that individuals are continually arriving despite the temperature gradient and their vulnerability to predators in the ditch. Speckled dace may venture out to feed at night, the time they are most active in the creek, but the other fishes are more active during the day (unpublished data). The healthy appearance of all fish indicates they are not starving under tunnel conditions.

This study also shows that the attempts to block Bly Tunnel to keep it from draining Eagle Lake have been at best only partially successful. The comparatively low flows now coming out of the tunnel may simply be the result of low lake levels following a long series of dry years. If the lake level rises again, outflow of the tunnel should be monitored and further attempts made to block the outflow if it is found to be keeping the lake at an artificially low level.

ACKNOWLEDGMENTS

We appreciate the cooperation and assistance of Raymond J. Bogiatto, director of the Eagle Lake Field Station, California State University, Chico, as well as the help and hospitality of Robert and Teri Smith. J. Noah Moyle and Marilyn A. Moyle assisted in the collection of the fish.

LITERATURE CITED

AMESBURY, R. 1971. Eagle Lake. Privately published, Susanville, California.

BUSAK, C. A., G. A. THORGAARD, M. P. BANNON, AND G. A. E. GALL. 1980. An electrophoretic, karyotypic, and meristic characterization of the Eagle Lake trout. Copeia 1980: 418–424.

HUNTSINGER, K. R., AND P. E. MASLIN. 1976. A limnological comparison of the three basins of Eagle Lake, California. California Fish and Game 62: 232–245.

HYNES, H. B. N. 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. Journal of Animal Ecology 19: 36–58.

MOYLE, P. B. 1976. Inland fishes of California. University of California Press, Berkeley. 402 pp.

PURDY, T. I. 1988. Purdy's Eagle Lake. Lahonton Images, Susanville, California.

Received 28 November 1990
Revised 25 April 1991
Accepted 13 May 1991

Great Basin Naturalist 51(3), 1991, pp. 271–278

HEAVY METAL TOLERANCE OF INLAND SALTGRASS (*DISTICHLIS SPICATA*)

R. A. Prodgers[1] and W. P. Inskeep[2]

Abstract.—Inland saltgrass (*Distichlis spicata*) occurs on at least two metal-contaminated sites in southwestern Montana. As a result of mining, milling, and smelting activities, soils have elevated concentrations of copper, zinc, and manganese. One soil is acidic (upper horizons), slightly saline, and moderately sodic. The other soil is alkaline, nonsaline, and nonsodic. The fact that inland saltgrass grows on these soils and does not accumulate dangerous levels of metals makes it a candidate species for revegetating hardrock mining and other metal-polluted sites.

Key words: inland saltgrass, Distichlis spicata, *preadaptation, metal-contaminated soils.*

Distichlis spicata (L.) Green var. *stricta* (Torr.) Beetle, commonly known as inland saltgrass, is a perennial, shallow-rooted, warm-season grass that grows from hard, scaly rhizomes. Palatability is low but is enhanced by heavy cropping, which also promotes a dense sod (Weaver 1954).

D. spicata is most commonly found on moist saline soils in the Great Plains. Daubenmire (1974) referred to inland saltgrass as an example of plant zonation around a saline basin; saltgrass was found in the wettest and saltiest sites occupied by vascular plants. Elsewhere, other species may exhibit greater salt tolerance (Dodd et al. 1964, Unger 1974). The soil salt content associated with saltgrass communities can range at least from 0.03 to 5.6% (Ungar 1974). Inland saltgrass can tolerate an average soil electrical conductivity (EC) of 66 mmhos/cm in the upper 10 cm of soil (Ungar 1969). However, in mixed-prairie communities where saltgrass is abundant in east central Montana, saltgrass occur on soils with ECs of ≤ 2 (Prodgers 1978). Saltgrass abundance appears to increase in response to grazing intensity in mixed communities adjacent to more saline sites.

The relative abundance of cations and anions in soils of saltgrass communities varies with soil horizon and site. The predominant cation is usually sodium, but magnesium, potassium, or calcium may be abundant (Dodd et al. 1964, Dodd and Coupland 1966a, Ludwig and McGinnies 1978). Principal anions are sulfate, bicarbonate, and chloride.

Prodgers (1978) reported sodium adsorption ratios (SARs) >60 for saltgrass community soils. Ludwig and McGinnies (1978) reported an SAR of 4 in the A horizon and 79 in the C horizon. Soil pHs for inland saltgrass communities commonly range from 7 to 10 (Poole 1980).

The ability of saltgrass to grow on salty sites may depend on its ability to exclude salts. *Distichlis spicata* can survive salt-stressed environments by a process in which vacuolar compartmentation of salt is followed by osmotic compartmentation in the cytoplasm via an organic solute such as proline (Daines and Gould 1985). Inland saltgrass maintains high osmotic pressure in the cell sap. Dodd and Coupland (1966b) measured osmotic pressures in *D. spicata* of 22–48 atmospheres in a saline meadow community. This suggests that the membranes of saltgrass can extract water from the matrix of saline soils. Efficient membranes might also exclude salts and metals from critical sites in the plant. *Distichlis* has been reported to secrete salts, allowing it to survive what would otherwise be excessive ionic accumulation (Frey-Wyssling 1935, as cited in Ungar 1974).

We speculate that salt-excluding mechanisms may preadapt saltgrass to grow on metal-rich sites and suggest that, if so, saltgrass might be planted on metal-contaminated sites to provide cover. Due to the rhizomatous growth form, saltgrass spreads vegetatively and controls soil erosion. Low

---

[1] 2715 Ottawa, Butte, Montana 59701.
[2] Department of Plant and Soil Science, Montana State University, Bozeman, Montana 59717.

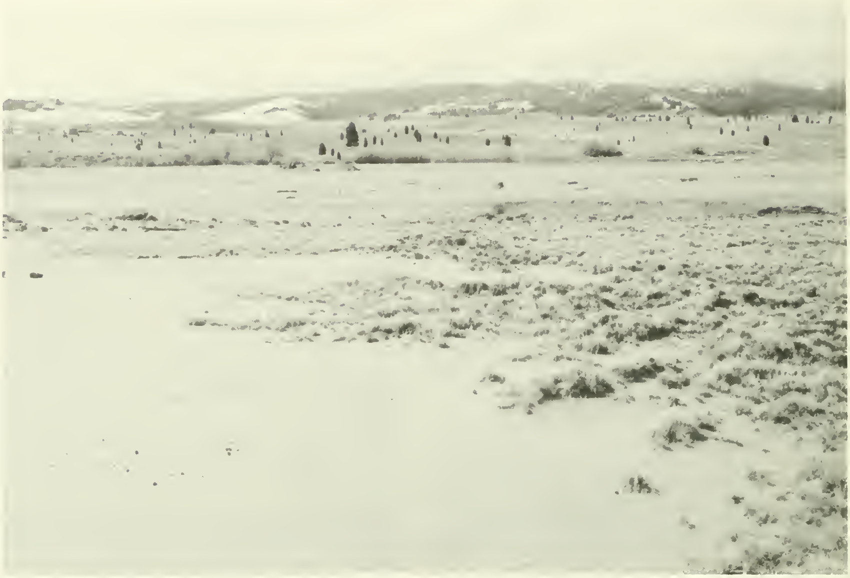


Fig. 1. Inland saltgrass community on streambank tailings near Ramsay, Montana. Floods deposited tailings and mining detritus along stream. Contagious distribution of vegetatively spreading saltgrass community is evident.

palatability is desirable for revegetation of metal-contaminated sites.

To determine the metal tolerance and metal-excluding capabilities of saltgrass, we measured the metal concentrations of saltgrass tissues and associated soils at two contaminated sites. Comparison is made between acceptable metal levels in livestock forage and normal metal concentrations in soils.

SITES AND METHODS

Two *Distichlis spicata* communities were investigated on metal-rich soils in southwestern Montana. One community is situated on stream-deposited hardrock mine tailings along Silver Bow Creek near Ramsay, Montana, Section 22, T3N, R9W, at an elevation of 1615 m (Fig. 1). The tailings originated at upstream milling and smelting operations along the creek from 1860 to 1910. A series of floods in the 1890s and a major flood in 1908 washed tailings into the creek. Subsequent floods since 1908 (particularly in 1948, 1975, 1980, and 1981) have re-deposited tailings along the creek (CH2M Hill 1989). These tailings deposits now occur along the creek in distinctively colored strata, most of which are rich in heavy metals and low in pH due to pyrite oxidation. Some taller plants, such as willows, have survived tailings deposits, but shorter vegetation was buried and current grass and forb plant communities represent colonization by adapted species.

The second community occurs on an upland Mollisol derived from frost-worked travertine a few hundred meters from the copper smelter stack near Anaconda, Montana, in Section 12, T4N, R11W, at an elevation of 1740 m (Fig. 2). This site has received heavy metal deposits and sulfur dioxide fumigation from the smelter stack dating roughly from 1900 to 1980. Vegetation within several miles of the stack has been dramatically affected by stack emissions. Erosion from a nearby road has resulted in soil deposition in the *Distichlis spicata* community. Inland saltgrass does not typically occur on upland Mollisols.

Three soil pits were located to encompass surficial variability within each community.

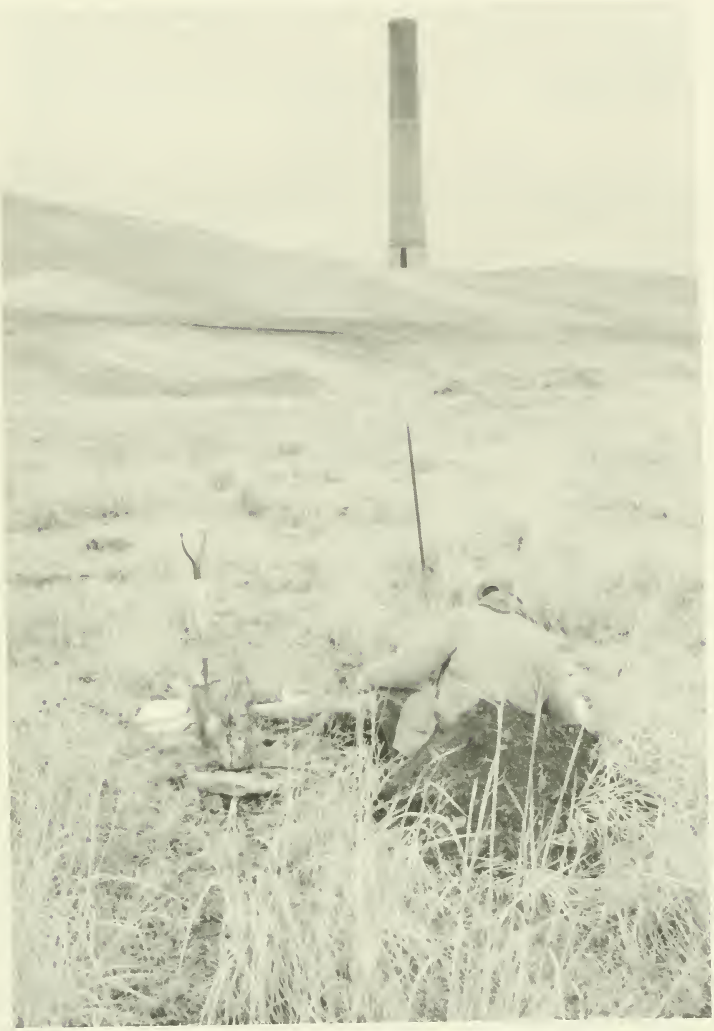


Fig. 2. Inland saltgrass–Great Basin wildrye plant community near copper smelter at Anaconda, Montana. Although Great Basin wildrye is more conspicuous in the photo due to its height, saltgrass has greater canopy coverage. Heavy metals in soils were deposited as airborne fallout from the copper smelter (background) and through deposition of erosional sediments.

Soil profiles were described and .5 kg of soil was collected from each horizon at each pit. Particle size was determined following the procedure of Day (1965). Electrical conductivity, SAR, and pH were determined from saturated paste extracts. Soils were digested in 4M HNO_3 at 70 C overnight (Chang et al. 1987) for total analysis of copper, manganese, and zinc. Extractable metal concentrations were determined using DTPA (Lindsay and

TABLE 1. Profile description for streambank mine tailings soil near Ramsay, Montana.

Horizon	Depth (cm)	Texture	Structure	Consistency	Roots	pH[a]	EC[a] (mmhos/cm)	SAR[a]
A	0–13	very fine sandy loam	massive	slightly hard very friable nonsticky, nonplastic	none (underground culms)	4.0–4.9	4–8	1–4
C1	13–20	fine and very fine sandy loam	massive	soft very friable nonsticky, nonplastic	culms, rhizomes, very few medium, fine, and very fine roots	5.4–7.6	4–8	2–5
C2	20–33	very fine sandy loam	massive	hard very friable nonsticky, nonplastic	common medium, few fine and very fine roots	5.4–7.6	4–8	2–5
Ab	33–46	very fine sandy loam	massive	slightly hard friable slightly sticky, slightly plastic	few rhizomes, few fine and very fine roots	6.5–7.6	2–10	2–9
C1b	46–74	silt loam	massive	soft friable slightly sticky, slightly plastic	few fine and very fine roots	7.8–7.9	1–7	2–13
C2b	74–100	silt loam	massive	slightly hard friable slightly sticky, slightly plastic	few fine and very fine roots	7.8–7.9	1–7	2–13
2Cb	100–127	very fine sandy loam	massive	soft friable nonsticky, nonplastic	very few fine and very fine roots	7.5–8.0	1–3	3–18

[a] Ranges based on three field subsamples of each horizon.

Norvell 1969, Soltanpour et al. 1976) in the absence of triethanolamine. Copper, zinc, and manganese concentrations in digestates and DTPA extracts were analyzed using inductively coupled plasma emission spectroscopy (ICP).

Soil profile descriptions are summarized in Tables 1 and 2. At the streambank tailings site, near-surface horizons are acidic, but pH increases in the deeper, poorly aerated horizons. These tailings generate acid in an oxidized environment. This soil is slightly saline, but sodium is not excessive, although borderline in some horizons. At the smelter site, where the soil parent material is frost-worked travertine, pH is slightly alkaline, the soil is nonsaline, and due to the predominance of calcium, SARs are <1.

Plant communities were sampled by estimating canopy coverage (Daubenmire 1959) in 20 × 50-cm quadrats placed at 1-m intervals (smelter) or 3-m intervals (tailings) along linear transects. Due to the shapes of the plant communities, the tailings *D. spicata* community was sampled along a single 75-m transect ($n = 25$), whereas the smelter community was sampled along three transects with total length of 40 m ($n = 40$). The larger sample size was appropriate for the more heterogeneous community at the smelter site. Aboveground plant tissue samples were clipped above 3 cm at random intervals along transects, separated into foliage and inflorescences, oven-dried at 70 C, chopped, digested in nitric-perchloric acid, and analyzed with ICP (Havlin and Soltanpour 1980). Inflorescences make up a small portion of saltgrass production in most years.

TABLE 2. Profile description for soil near copper smelter at Anaconda, Montana.

Horizon	Depth (cm)	Texture	Structure	Consistency	Roots	pH[a]	EC[a] (mmhos/cm)	SAR[a]
A	0–8	very fine sandy loam	massive	soft very friable slightly sticky, slightly plastic	few stems, rhizomes	7.4–8.0	0.6–0.8	0.2
Ab	8–25	gravelly very fine sandy loam	moderate medium angular blocky	soft very friable slightly sticky, slightly plastic	few fine and very fine roots	7.2–7.8	0.3–1.1	0.1–0.2
Bw	24–25+	gravelly very fine sandy loam	massive	soft very friable nonsticky, nonplastic	common fine and very fine roots	7.5–8.1	0.4–0.9	0.2

[a]Ranges based on three field subsamples of each horizon.

TABLE 3. Species composition of two *Distichlis spicata* var. *stricta* communities.

	Streambank tailings site		Copper smelter site	
Species	Canopy coverage	Frequency	Canopy coverage	Frequency
	%			
Agrostis sp.	NP[a]		0.1	2
Distichlis spicata	32.6	92	32.8	95
Elymus cinereus	NP		17.0	60
Juncus balticus	1.0	4	NP	
Muhlenbergia asperifolia	NP		0.1	2
Tetradymia canescens	NP		1.9	5
Litter	39.7	100	45.3	100
Bare soil	49.3	100	21.6	95
Surficial rock fragments[b]	NP		3.8	52

[a] NP = not present.
[b] >2 mm.

Plant community compositions are summarized in Table 3. *Distichlis spicata* is the sole dominant species in the community located on the streambank tailings. At the smelter site, the much taller *Elymus cinereus* is subdominant in coverage, and several other species are present. *Elymus cinereus*, *Muhlenbergia asperifolia*, and *Tetradymia canescens* are more abundant at other sites near the smelter than is *D. spicata*.

RESULTS AND DISCUSSION

Metal Concentrations of Soils

Tables 4 and 5 present mean concentrations of Cu, Zn, and Mn by soil depth at each site. Subsample concentrations of metals for each depth increment varied, thus the rather large variance. Three replicates of one soil sample were analyzed concurrently with other total and extractable metal determinations. The average coefficients of variation for extractable and total metal determinations were 3.0% and 3.4%, respectively, demonstrating good precision for laboratory techniques. Therefore, the high variability in metal concentrations from proximate soil samples appears to be due to variations in alluvial deposits rather than imprecise analysis.

At the smelter site, total and available metal concentrations decrease with depth as expected for pollutants deposited on the surface (Table 4). Root distribution was difficult to quantify due to the presence of 20–35% rock fragments, but roots were scarce below .5 m. Flagstones often terminated root penetration and resulted in concentrations of roots immediately above the flagstones. The A horizon contained mostly stems and some rhizomes, so roots were most abundant in the Ab and Bw horizons (8–45+ cm).

TABLE 4. Heavy metal concentrations in copper smelter soil supporting *Distichlis spicata* (means and standard deviations).

Depth (cm)		Cu	Zn	Mn
		µg/g soil		
0–8	Total	3600 ± 980	2600 ± 520	1200 ± 130
	DTPA	410 ± 52	180 ± 47	2.8 ± 2.1
8–25	Total	1900 ± 650	1400 ± 480	780 ± 160
	DTPA	320 ± 150	200 ± 37	11 ± 14
25–45+	Total	410 ± 180	500 ± 170	570 ± 69
	DTPA	190 ± 110	200 ± 50	13 ± 17

TABLE 5. Heavy metal concentrations in alluvial tailings soil supporting *Distichlis spicata* (means and standard deviations).

Depth (cm)		Cu	Zn	Mn
		µg/g soil		
0–13	Total	3700 ± 1200	1700 ± 480	1700 ± 510
	DTPA	800 ± 220	240 ± 72	170 ± 76
13–33	Total	13,000 ± 3600	5700 ± 1700	5300 ± 1200
	DTPA	690 ± 190	130 ± 80	68 ± 42
33–46	Total	9200 ± 7300	6200 ± 4800	4900 ± 6400
	DTPA	440 ± 290	86 ± 50	41 ± 35
46–100	Total	340 ± 250	410 ± 420	710 ± 380
	DTPA	43 ± 30	26 ± 27	31 ± 13
100–127	Total	120 ± 73	67 ± 40	310 ± 200
	DTPA	15 ± 30	3.9 ± 2.5	11 ± 6.1

At the streambank tailings site, the depositional sequence of varied tailings materials and subsequent migration of soluble metals have resulted in the highest metal concentrations in the zone where roots are most abundant (13–46 cm depth). Metal concentrations were lower in the surface horizon (0–13 cm) where underground stems and rhizomes were well represented but few roots occurred. Metal concentrations were lowest in the 46–127-cm-depth interval, where roots were less common than higher in the profile.

Total Cu concentrations in the upper 46 cm at the streambank tailings site and upper 8 cm at the smelter site were 100 or more times higher than "normal" soils. Total Cu concentrations in soils summarized by Adriano (1986) averaged 30 µg Cu/g soil, ranging from 2 to 250 µg Cu/g soil. Total Cu concentrations in samples of soils in Japan ranged from 4 to 176 µg Cu/g soil (Iimura 1981). In Japan the legal limit of Cu in agricultural soils is 125 ppm (based on 0.1 N HCl extraction), as stipulated in the Agricultural Land Soil Pollution Prevention Law (Chino 1981).

Total Zn concentrations in the upper horizons of the studied saltgrass soils were roughly 15 to 70 times higher than average. Adriano (1986) reported total Zn concentrations ranging from 1 to 900 µg Zn/g soil; the average was 90 µg Zn/g soil. Soil samples from Japan contained 10 to 662 µg Zn/g soil (Iimura 1981).

Total Mn concentrations reported in Tables 4 and 5 range from normal to about 10 times higher than usual. Total Mn concentration in soils reported by Shacklette et al. (1971) averaged 560 µg Mn/g soil, with values ranging from 1 to 7,000 µg Mn/g soil. In another summary, the mean total Mn content of surface soils ranged from 80 to 1,315 µg Mn/g soil (Kabata-Pendias and Pendias 1984).

In a different study conducted near East Helena, Montana, soils were sampled and mapped on the basis of metal contamination from a smelter located in East Helena, which is about 89 km northeast of the study sites reported here. Soils that presumably were unaffected by smelter pollution had geometric mean DTPA-extractable concentrations in the upper 38 cm of soil of approximately

TABLE 6. Heavy metal concentrations in foliage of *Distichlis spicata* and *Elymus cinereus* grown on soils described in Tables 1, 2, 4, and 5.

Site	Species	Cu	Zn	Mn
		µg/g tissue		
Tailings	*D. spicata*			
	Inflorescence	490	490	430
	Foliage	130	230	150
Smelter	*D. spicata*			
	Inflorescence	260	190	45
	Foliage	94	120	25
	E. cinereus			
	Foliage	87	91	39

1 mg/kg Cu, 15 mg/kg Mn, and <0.1 mg/kg Zn (CH2M Hill 1987). The soils reported here contain far more Cu and Zn than these background concentrations.

In summary, comparisons of our data with those reported in the literature demonstrate that the upper .5 m of soil at the streambank tailings site had very high concentrations of all three metals. The smelter soil had very high Cu and Zn concentrations, but not Mn.

Metal Concentrations of Foliage

Foliar metal concentrations of *Distichlis spicata* and *Elymus cinereus* were similar; however, *D. spicata* inflorescences accumulated higher metal concentrations, particularly Cu, than did foliage (Table 6).

Plant shoots usually do not accumulate more than 200 µg Cu/g foliage (dry weight), a concentration often considered the threshold value above which plant injury may occur (Kabata-Pendias and Pendias 1984). Maximum tolerable levels of Cu in forage (total diet) for cattle, sheep, and horses are 100, 25, and 800 µg/g of forage, respectively (NAS 1980). These values are based on residues in human food as well as animal health. Foliar concentrations reported in Table 6 are unacceptable for sheep, marginal for cattle, and acceptable for horses, since horses are not generally considered a meat source in the United States.

The maximum tolerable diet concentration of Mn for cattle and sheep is 1000 µg Mn/g forage (NAS 1980). Many plant species are affected by Mn concentrations around 500 µg Mn/g tissue (dry weight), but resistant species or races can tolerate concentrations above 1000 µg/g. The foliar Mn concentration of saltgrass (Table 6) is acceptable for livestock.

Animals are tolerant of high Zn levels in their diet (National Research Council 1979). Maximum tolerable diet concentrations of Zn are 500 µg Zn/g forage for cattle and 300 µg Zn/g forage for sheep (NAS 1980). Cereal grains and vegetables usually contain less than 50 µg Zn/g tissue (Kabata-Pendias and Pendias 1984). While elevated, the foliar Zn concentration of saltgrass is acceptable for livestock grazing.

Considering the very high metal concentrations in the soil, *D. spicata* appears largely to exclude these metals from foliage. Only the Cu concentrations are near or above levels that might pose a problem if humans consumed livestock that grazed solely on foliage grown on heavily contaminated soils from the affected areas. However, livestock ingestion of contaminated soils could greatly increase livestock intake of heavy metals, particularly when a short-grass such as inland saltgrass is grazed. For this reason, livestock grazing of heavily contaminated sites is not recommended. Under open-range grazing conditions, unpalatable species are desirable for revegetation of metal-contaminated sites.

The preadaptation of saltgrass for metal-rich sites, its low palatability, and its soil-binding characteristics make *D. spicata* an attractive grass for revegetation of appropriate sites. Special metal-tolerant varieties could be developed from genotypes present on sites such as those reported here. In current revegetation practices, *D. spicata* is usually propagated from rhizomes due to problems with germination and seedling emergence; however, seeding is much cheaper and more convenient. Stratification and scarification treatments can increase naturally low germination (Cluff et al. 1983). Metal-tolerant races of inland saltgrass have potential for revegetation of metal-contaminated areas in the West if establishment from seed proves to be practical.

LITERATURE CITED

ADRIANO, D. 1986. Trace elements in the terrestrial environment. Springer-Verlag, New York. 533 pp.

CHANG, A., A. PAGE, AND J. WARNEKE. 1987. Long-term sludge applications on cadmium and zinc accumulations in Swiss chard and radish. Journal of Environmental Quality 16: 217–221.

CH2M HILL. 1987. Remedial investigation of soils, vegetation, and livestock for East Helena site (ASARCO), East Helena, MT. EPA Work Assignment No. 68-8L30.0. 436 pp.

______. 1989. Silver Bow Creek flood modeling study—Nov. 30, 1989. Document BO120840. 85 pp.

CHINO, M. 1981. Metal stress in rice plants. Pages 65–80 *in* Heavy metal pollution in soils of Japan. Japan Scientific Society Press, Tokyo. 302 pp.

CLUFF, G., G. EVANS, AND J. YOUNG. 1983. Desert saltgrass seed germination and seedbed ecology. Journal of Range Management 36: 419–422.

DAINES, R., AND A. GOULD. 1985. The cellular basis of salt tolerance studies with tissue cultures of the halophytic grass *Distichlis spicata*. Journal of Plant Physiology 199: 269–280.

DAUBENMIRE, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33: 43–64.

______. 1974. Plants and environment. 3rd ed. John Wiley & Sons, New York. 422 pp.

DAY, D. 1965. Particle-size fractionation and particle-size analysis. Pages 545–566 *in* Methods of soil analysis, part I. Physical properties and mineralogical properties, including statistics of measurement and sampling. American Society of Agronomy, Madison, Wisconsin.

DODD, J., AND R. COUPLAND. 1966a. Vegetation of saline areas in Saskatchewan. Ecology 47: 958–968.

______. 1966b. Osmotic pressures of native plants of saline soils in Saskatchewan, Canada. Journal of Plant Science 46: 479–485.

DODD, R., D. RENNIE, AND R. COUPLAND. 1964. The nature and distribution of salts in uncultivated saline soils in Saskatchewan. Canadian Journal of Science 44: 165–175.

HAVLIN, J. L., AND P. N. SOLTANPOUR. 1980. A nitric acid plant tissue digest method for use with inductively coupled plasma spectrometry. Communications in Soil Science and Plant Analysis 11: 969–980.

IIMURA, K. 1981. Background content of heavy metals in Japanese soils. Pages 19–26 *in* Heavy metal pollution in soils of Japan. Japan Scientific Society Press, Tokyo. 302 pp.

KABATA-PENDIAS, A., AND H. PENDIAS. 1984. Trace elements in soils and plants. CRC Press, Boca Raton, Florida. 315 pp.

LINDSAY, W., AND W. NORVELL. 1969. Development of a DTPA micronutrient soil test. Agronomy Abstracts 69: 84.

LUDWIG, J., AND W. MCGINNIES. 1978. Revegetation trials on a saltgrass meadow. Journal of Range Management 31: 308–311.

NATIONAL ACADEMY OF SCIENCES (NAS). 1980. Mineral tolerance of domestic animals. Washington, D.C. 577 pp.

NATIONAL RESEARCH COUNCIL. 1979. Zinc. Medical and biological effects of environmental pollutants. University Park Press, Baltimore, Maryland. 471 pp.

POOLE, B. 1980. Biota of the northern Rockies: a review of *Distichlis spicata*. Proceedings of the Montana Academy of Science 39: 89–96.

PRODGERS, R. 1978. Circle West vegetation and baseline study. Montana DNRC Technical Report No. 1. 115 pp.

SHACKLETTE, H., J. HAMILTON, J. BOERNGEN, AND J. BOWLES. 1971. Elemental composition of surficial materials in the conterminous United States. USGS Professional Paper 574-D. Washington, D.C. 71 pp.

SOLTANPOUR, P., A. KHAN, AND W. LINDSAY. 1976. Factors affecting DTPA-extractable Zn, Fe, Mn, and Cu from soils. Communications in Soil Science and Plant Analysis 7: 797–821.

UNGAR, I. 1969. Plant communities of saline soils at Lincoln, NE. American Midland Naturalist 78: 98–120.

______. 1974. Inland halophytes of the United States. *In:* W. H. Queen, ed., Ecology of halophytes. Academic Press Inc. 605 pp.

WEAVER, J. 1954. North American prairie. Johnsen Publication Company, Lincoln, Nebraska. 348 pp.

Received 6 February 1991
Revised 12 July 1991
Accepted 15 July 1991

Great Basin Naturalist 51(3), 1991, pp. 279–281

NOTES ON CRYPTOGAMIC PLANTS OF UTAH: RANGE EXTENSIONS AND SPECIES NEW TO THE STATE FROM CAPITOL REEF NATIONAL PARK

John R. Spence[1]

Key words: cryptogamic plants, Capitol Reef National Park, Utah, Wayne County, Garfield County.

A recent floristic survey of Capitol Reef National Park, situated in Wayne and Garfield counties in south central Utah, has added many species to its flora (Heil 1990), including numerous rare and endangered species. Because of the great diversity in landforms, elevations, and attendent topographic relief, portions of the Waterpocket Fold in the park have been found to harbor a remarkable number of rare species as well as disjuncts from other areas in the state and the western U.S. (Spence 1987). Several of these are bryophytes, which as a group have less well known distributions in the western U.S. than the vascular plants (Spence 1988).

Additional fieldwork during the 1989–90 season has located several species either new to the state or to Wayne County and Capitol Reef National Park. These include the fern *Dryopteris filix-mas*, and the mosses *Abietinella abietina* and *Leskeella nervosa*. A major range extension is also noted for the moss *Isopterygium pulchellum*. Below, each of the new reports is discussed, along with habitat information, associated species, and regional significance.

The park has a semiarid climate, with hot summers and moderately cold winters. At park headquarters in Fruita (1675 m), average annual precipitation is 18.3 cm, with about 30% falling as late-summer (July–August) thunderstorms. The average July maximum temperature is 19.1 C, while the average January minimum is −21.9 C (park service data, 1948–1986).

Abietinella abietina (Hedw.) Fleisch.

UTAH: Wayne Co., Capitol Reef National Park, on dry, shaded Kaibab limestone under *Pseudotsuga menziesii*, middle part of Fremont Gorge, with *Symphoricarpos oreophilus* and *S. longiflorus*. Ele. 1800 m, 38°16′N, 111°17′W, T29S R6E Sec. 21. October 6, 1989. Spence 4104 (deposited in park herbarium).

This is the first report of living material of this species for Utah. The closest known locality for *Abietinella abietina* is a population in Dinosaur National Monument, Moffat County, Colorado (Flowers 1973). The park locality is an unusual habitat for the species, as it is in a relatively low-elevation, semiarid canyon. In the Pacific Northwest *Abietinella* is common at montane and subalpine elevations in the drier parts of the Cascade and Coast mountains (Lawton 1971). The species is found occasionally on dry rock over a wide elevational range in Colorado (Weber 1973).

The stand of Douglas-fir under which the moss was found may be relictual, as it is isolated elevationally from the main forest populations in south central Utah, which usually occur above 2100 m. The distribution and nature of this, as well as other isolated Douglas-fir stands on the Colorado Plateau (e.g., Brotherson et al. 1985, Tuhy and MacMahon 1988), suggest that they may be late Pleistocene–early Holocene relicts. The presence of *Abietinella abietina*, a boreal-arctic moss most common at montane to subalpine elevations in the western U.S., supports this. Remarkably, Betancourt (1984) has reported rare macrofossil material of *Abietinella* from Allen Canyon and Fishmouth Caves, ca. 140 km to the southeast of Capitol Reef National Park and near the Abajo Mountains, with radiocarbon ages of 3000–11,000 years and 3700 years, respectively. At least in the Allen Canyon Cave sequence, all packrat middens with *Abietinella* macrofossils also contained *Pseudotsuga menziesii* material.

---

[1] Manzanita BioStudies, 59D Fruita Lane, Capital Reef National Park, Torrey, Utah 84775.

Isopterygium pulchellum (Hedw.) Jaeg. & Sauerb.

UTAH: Wayne Co., Capitol Reef National Park. On dry, shaded vertical face of Wingate Sandstone, side canyon of Cohab Canyon, near campground. With *Fissidens bryoides* and *Pseudoleskella tectorum*. Ele. 1750 m, 38°17′N, 111°14′W, T29S R6E Sec. 23. November 2, 1989. Spence 4118. Also on dry Navajo Sandstone in shaded, humid crevice, just south of Blowout Flats, northeast of Golden Throne. With *Dryopteris filix-mas*, *Desmatodon obtusifolius*, *Pohlia nutans*, and *Amblystegium serpens* var. *juratzkanum*. Ele. 2000 m, 38°14′N, 111°11′W, T30S R7E Sec. 4. May 24, 1990. Spence 4135a (both deposited in park herbarium).

Isopterygium pulchellum has been reported once before from Utah (Summit County, Uinta Mountains, at an elevation of 2713 m; Flowers 1973). In western North America, it is most common on humid, shaded wood and soil in coniferous forests and is restricted to high-elevation spruce-fir forests in the southern Rocky Mountains (Ireland 1969, Lawton 1971, Weber 1973). The habitat the plants grew in, shaded Navajo and Wingate sandstones in a semiarid climate, is highly unusual for this species. The plants were restricted to the deepest, most heavily shaded recesses of cracks and are probably never exposed to direct sunlight. They appear to survive only because of a combination of shading and funneling of precipitation into the cracks from rock faces above.

Leskella nervosa (Brid.) Loeske

UTAH: Wayne Co., Capitol Reef National Park. On thin, dry, shaded soil on ledge of Navajo Sandstone, amphitheater directly north of Pioneer Register and west of Capitol Gorge Tanks. With *Petrophytum caespitosum* and *Selaginella mutica*. Ele. 1800 m, 38°16′N, 111°17′W, T30S R7E Sec. 9. October 24, 1989. Spence 4109a (deposited in park herbarium).

In a recent revision of *Pseudoleskeella*, Wilson and Norris (1989) reported *P. sibirica* (Arn.) P. Wilson & Norris (= *Leskeella nervosa* var. *sibirica*) from Utah and distinguished it from *P. nervosa* using leaf and asexual reproductive characters. Using their key, I was able to clearly identify the park plants as *P. nervosa*, inasmuch as they possess asexual brood bodies and the leaves on the upright branches have a strong costa extending somewhat obscurely into the acumen. This is the first report of *Leskeella (Pseudoleskeella) nervosa* for Utah. As it is found in Arizona, California, and Idaho, its presence in Utah is not unexpected. I agree that *Leskeella* and *Pseudoleskeella* are very close (Wilson and Norris 1989); however, I prefer to maintain them as separate genera for now, based on the occurrence of asexual brood bodies in the former but not the latter.

Dryopteris filix-mas (L.) Schott

UTAH: Wayne Co., Capitol Reef National Park. In humid crevice in Navajo Sandstone, just south of Blowout Flats northeast of Golden Throne. With *Cymopterus beckii*, *Erigeron maguirei*, *Desmatodon obtusifolius*, *Pohlia nutans*, and *Amblystegium serpens* var. *juratzkanum*. Ele. 2000 m. 38°14′N, 111°11′W, T30S R7E Sec. 4. July 23, 1990. Spence & Mason 4137 (deposited in park herbarium).

New to Wayne County and Capitol Reef National Park, *Dryopteris filix-mas* has been collected in five other localities in Utah, once each in Garfield, Sanpete and Salt Lake counties, and twice in Washington County (Albee et al. 1988). The closest population is the one in Garfield County. The park plants were growing in a narrow, shaded crevice in Navajo Sandstone in an area of high topographic relief in the Waterpocket Fold of the park, just south of a pristine aeolian grassland/*Pinus ponderosa* woodland complex called Blowout Flats. Three rare species, *Erigeron maguirei* (listed endangered), *Gilia caespitosa* (category 1 species), and *Cymopterus beckii* (category 2 species), were also growing in the crevice. *Dryopteris* is a common circumboreal fern, abundant in the Pacific Northwest and the northern Rocky Mountains. Further south, it is found in scattered localities in the mountains south to New Mexico and Arizona (Cronquist et al. 1972). The habitat of the park population, at middle elevations in semiarid slickrock, is atypical compared with traditional northern habitats.

DISCUSSION

All species in this report are rare in Utah and Capitol Reef National Park. The mosses are sterile, while *Dryopteris* produces abundant sori. Unusual habitats, rarity, and disjunct distribution patterns suggest that all these species are relicts from a previous period when climates in the region were milder and wetter, probably the late Pleistocene or early Holocene (Betancourt 1984). All are associated with species, including *Pinus ponderosa*, *Symphoricarpos oreophilus*, *Petrophytum caespitosum*, *Arctostaphylos patula*, *Cymopterus beckii*, and *Gilia caespitosa*, which are at or below their typical lower elevational limits in south central Utah (Welsh et al. 1987). For example, small stands of *P. ponderosa* are found as low as 1800 m in the Fold, where they consist almost exclusively of large (>50 cm dbh) and presumably old trees with little or no recruitment occurring (Spence, unpublished data). The trees are isolated by low elevations (1500 m to the west and 1400 m to the east) and semiarid to arid shrublands from the extensive *P. ponderosa* forests on the Henry, Boulder and Thousand Lake mountains. Populations of these species may be stranded relicts from the late Pleistocene, surviving in the Waterpocket Fold only because of its large vertical relief (700 m) and varied topography and substrates. The fern and mosses can be considered rare components of these relict vegetation patches.

ACKNOWLEDGMENTS

The National Park Service and Capitol Reef Natural History Association provided support and housing, for which I am grateful. Many thanks to Norm R. Henderson, Resource Management, who supported and encouraged my work in the park.

LITERATURE CITED

ALBEE, B. J., L. M. SCHULTZ, AND S. GOODRICH. 1988. Atlas of the vascular plants of Utah. Utah Museum of Natural History, Salt Lake City.

BETANCOURT, J. L. 1984. Late Quaternary plant zonation and climate in southeastern Utah. Great Basin Naturalist 44: 1–35.

BROTHERSON, J. D., W. E. EVENSON, S. R. RUSHFORTH, J. FAIRCHILD, AND J. R. JOHANSEN. 1985. Spatial patterns of plant communities and differential weathering in Navajo National Monument. Great Basin Naturalist 45: 1–13.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora. Vol. 1. Hafner Publishing Company, Inc., New York.

FLOWERS, S. 1973. Mosses: Utah and the West. Brigham Young University Press, Provo, Utah.

HEIL, K. D. 1990. Flora of Capital Reef National Park. Unpublished manuscript.

IRELAND, R. R. 1969. A taxonomic revision of the genus *Plagiothecium* for North America, north of Mexico. National Museums of Canada, National Museum of Natural Science Publications in Botany No. 1: 1–118.

LAWTON, E. 1971. Moss flora of the Pacific Northwest. Nichinan, Japan.

SPENCE, J. R. 1987. *Pseudocrossidium aureum* (Bartr.) Zander (Pottiaceae, Musci) new to Utah. Great Basin Naturalist 47: 347–348.

______. 1988. Checklist of the mosses of the Intermountain West, USA. Great Basin Naturalist 48: 394–401.

TUHY, J. S., AND J. A. MACMAHON. 1988. Vegetation and relict communities of Glen Canyon National Recreation Area. Final Report to the National Park Service, Glen Canyon National Recreation Area, Utah. The Nature Conservancy, Salt Lake City, Utah.

WEBER, W. A. 1973. Guide to the mosses of Colorado. Institute of Arctic and Alpine Research, University of Colorado, Occasional Paper No. 6: 1–48.

WELSH, S. A., N. D. ATWOOD, L. C. HIGGINS, AND S. GOODRICH. 1987. A Utah flora. Great Basin Naturalist Memoirs No. 9. 894 pp.

WILSON, P., AND D. H. NORRIS. 1989. *Pseudoleskeella* in North America and Europe. Bryologist 92: 387–396.

Received 15 January 1991
Revised 19 June 1991
Accepted 12 July 1991

Great Basin Naturalist 51(3), 1991, pp. 282–285

FACTORS INFLUENCING DISSOLVED OXYGEN CONCENTRATIONS DURING WINTER IN SMALL WYOMING RESERVOIRS

Paula M. Guenther[1] and Wayne A. Hubert[2]

Key words: dissolved oxygen, reservoir, winter, Wyoming.

Fish kills in ice-covered lakes have been described in the upper Midwest and the Great Plains (Nickum 1970, Patriarche and Merna 1970). Fish losses were related to low dissolved oxygen and several associated factors: small, shallow lakes; periods of prolonged or extensive snow and ice cover; lack of surface water inflow into lakes; and high primary productivity (Greenbank 1945, Halsey 1968, Nickum 1970, and Mathias and Barica 1980).

Miller (1989) investigated the geomorphic features that influence winterkill in natural lakes at elevations >2925 m in the Medicine Bow Mountains, Wyoming. He separated lakes prone to winterkill from those without a history of winterkill on the basis of six discriminating variables: basin area, basin relief ratio, lake area, drainage density, lake volume, and maximum water depth. Winterkill lakes tended to be small, shallow lakes and were at lower elevations than nonwinterkill lakes.

We assessed the winter dissolved oxygen concentrations in small reservoirs (<100 hectares at full pool) at elevations >2100 m above mean sea level. Physical, chemical, and climatic characteristics that are related to low dissolved oxygen under the ice were identified.

METHODS

Eleven reservoirs were studied during winter, 7 in 1987 and 10 in 1988 (Table 1). Six of the 1988 sites were also sampled the previous year. Study sites were selected to represent a range in elevation, size, and productivity. The reservoirs were located near or within the Laramie and Medicine Bow mountains in southeastern Wyoming. Several reservoirs had known histories of winterkill.

Bathymetric maps were obtained from the Wyoming State Engineer's Office or constructed from soundings that were plotted on reservoir outlines from U.S. Geological Service topographic maps. The maps were used to calculate morphometric variables: maximum water depth, mean water depth, water volume, and volume of unfrozen water during winter. Water levels were monitored to estimate the minimum values of the morphometric variables during winter.

Macrophyte abundance was estimated in fall 1987 for the 10 reservoirs to be studied. A 10-m line attached to a float was thrown from the shore at 10-m intervals around the reservoir. The density of plants along the line was visually estimated on a scale of 0 to 10. The presence or absence of plants beyond the line was noted and rated (0 = absent, 5 = present). Also, a reservoir-wide rating of filamentous algae was made (0 = absent, 3 = present, 5 = pervasive). The averages for the line and beyond-line ratings were summed with the rating for algae to yield Macrophyte Abundance Index (MAI) values ranging from 0 to 20.

Reservoirs were sampled at three-week intervals beginning in January and continuing until ice conditions were unsafe in March or April. Physical and chemical features were measured at one to four sites, depending on the reservoir size. Vertical profiles of dissolved oxygen concentrations were measured. The oxygen meter was standardized in

---

[1] U.S. Department of Agriculture Forest Service, Medicine Bow National Forest, Laramie, Wyoming 82070

[2] U.S. Fish and Wildlife Service, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, Wyoming 82071.

TABLE 1. Physical features of the reservoirs studied in southeastern Wyoming during the winters of 1986–87 and 1987–88. A range indicates variation between years.

Reservoir	Elevation (m)	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Inflow (1 = present, 0 = absent)
Crystal	2126	37	12.2	17.9	1
East Lake	2133	18	1.8	3.2	0
Shirley Basin	2135	6	3.0	4.2	0
Granite Springs	2199	21	11.7	15.3	1
Goforth	2207	2	1.4–1.6	2.2–2.5	1
Leazenby	2234	4–8	0.2–0.4	0.5–1.0	1
King Number 1	2247	50–58	1.4–1.6	3.0–3.5	1
North Crow	2311	14–17	8.9–11.8	12.6–17.1	1
Miller Lake	2763	1	1.6–2.0	2.5–3.0	1
Sucker Lake	3166	2	0.2	0.5	1
Dipper Lake	3261	9–11	1.8–2.8	9.0–10.5	0

the laboratory and calibrated in the field before each use. To verify the reading with the oxygen meter, we collected water samples at points along the profile with a Kemmerer sampler, fixed them immediately, and determined dissolved oxygen concentration using the Azide modification of the Winkler method (American Public Health Association et al. 1975).

Average dissolved oxygen was calculated for each sampling date. Each reservoir was divided into depth strata, and the water volume in each stratum was calculated. Average oxygen concentration in each stratum was computed, and an overall weighted total oxygen concentration was determined. Winterkill conditions were assumed to be likely when daytime average dissolved oxygen was <4 mg/L (Mathias and Barica 1980).

Water inflow and outflow were recorded as present or absent on each visit. Snow and ice thickness were measured, and the mean for all sampling dates was calculated.

Measurements of variables (Table 2) for the two winters were compared using paired *t* tests (Zar 1984). Correlation analysis was used to assess relations between measured variables and average dissolved oxygen concentrations. Stepwise multiple regression and discriminant function analysis were used to identify multivariate relations. We used the Number Cruncher Statistical System (Hintze 1987) to perform the statistical analyses. The critical level chosen for all statistical procedures was $P \leq .05$.

RESULTS

Substantial variation in elevation, surface area, and water depth during winter, and the presence of inflowing water were observed among the reservoirs (Table 1). Low dissolved oxygen (<4 mg/L) was common among the reservoirs (Table 2). Oxygen profiles showed typical stratification, highest concentrations being near the ice-water interface and lowest near the bottom of the reservoir. We observed average dissolved oxygen concentrations <4 mg/L in two reservoirs in 1987 (Dipper Lake and Miller Lake) and in five reservoirs in 1988 (Dipper Lake, Shirley Basin, East Lake, Goforth, and Miller Lake). Water in all reservoirs was saturated with oxygen at the beginning of the winter. We did not observe gradual depletion in dissolved oxygen over the winters.

Weather data from 1955 to 1988 showed that both the 1986–87 and 1987–88 winters were about average in temperature and precipitation. Our data suggest that the winter of 1987–88 was more severe than that of 1986–87. Average snow and ice were both significantly thicker in 1988 than in 1987. Although water levels were higher in 1988 than in 1987, more of the total water volume was in the form of ice. Because of the differing conditions between the two years, we treated each year as an independent sample.

Average dissolved oxygen concentration during winter was significantly ($P \leq .05$) correlated with the absence of inflow ($r = .56$), elevation ($r = -.49$), ice thickness ($r = -.56$), snow and ice thickness ($r = -.49$), and surface area of the reservoir during winter ($r = .49$). When Dipper Lake was excluded from the analysis, the MAI was highly correlated ($r = -.96$) with low dissolved oxygen levels.

TABLE 2. Conditions measured in the reservoirs studied in southeastern Wyoming during the winters of 1986–87 and 1987–88.

Reservoir	Mean dissolved oxygen (mg/L)	Minimum dissolved oxygen (mg/L)	Mean ice thickness (cm)	Mean snow thickness (cm)	Macrophyte abundance index
			1987		
Crystal	7.4	7.4	33	5	
Goforth	11.6	11.3	36	1	
Leazenby	12.4	12.2	32	1	
King Number 1	11.5	11.3	37	3	
North Crow	6.9	5.9	33	5	
Miller Lake	2.3	1.4	53	12	
Dipper Lake	1.5	1.1	111	82	
			1988		
East Lake	3.0	2.6	39	6	13
Shirley Basin	1.8	0.8	42	3	17
Granite Springs	8.7	7.1	38	3	3
Goforth	3.4	1.1	46	1	16
Leazenby	7.6	4.6	45	3	2
King Number 1	10.3	8.6	44	4	0
North Crow	6.9	5.9	33	5	5
Miller Lake	1.1	0.5	95	29	16
Sucker Lake	5.8	4.4	41	121	4
Dipper Lake	2.9	2.5	134	33	0

Stepwise multiple regression was used to determine variables that accounted for variation in average dissolved oxygen. The MAI was measured only in fall 1987, but we assumed that it remained constant over the years in our analysis. The most variability (adjusted $R^2 = .59$) in average dissolved oxygen (DO) among the reservoirs was accounted for by:

$$DO = 16.1 + 3.297\,I - 0.295\,M - 0.004\,E$$

where DO = average dissolved oxygen concentration (mg/L), I = 0 if no inflow and 1 if inflow was present, M = Macrophyte Abundance Index, and E = elevation (meters). All three independent variables were significant at $P \leq .05$.

Discriminant function analysis was used to classify reservoirs having average dissolved oxygen <4.0 mg/L from those that had ≥4.0 mg/L. It was possible to classify 16 of 17 samples based on three variables—presence or absence of inflow, mean winter ice thickness, and MAI. Reduction in classification error attributed to models in which these variables were used was 88%. Wilk's Lambda for the discriminant function was 0.14.

DISCUSSION

Our results indicate that the absence of inflowing water, high elevation, extensive ice and snow, small surface area, and abundant aquatic macrophytes contribute to low dissolved oxygen concentration during winter. Small (<20 ha during winter) reservoirs with no surface water inflow that are at high elevations or have abundant macrophytes (MAI > 12) have a high risk of developing low dissolved oxygen, and subsequently fish mortality, during winter. High risk of winterkill has been associated previously with small, shallow lakes, prolonged or extensive snow and ice cover, limited water inflow, and high primary productivity (Greenbank 1945, Halsey 1968, Nickum 1970, Barica and Mathias 1979, Mathias and Barica 1980).

No previous work has provided information for small reservoirs at >2100 m above sea level. Our findings may assist managers who are trying to prevent winterkill. Several of the variables identified as having an influence on dissolved oxygen during winter—absence of inflowing water, surface area, and the abundance of aquatic plants—may be manageable under various circumstances.

ACKNOWLEDGMENTS

We thank V. Hasfurther and R. Wiley for technical advice and R. Grost, D. Hubert, S. Kozel, S. Muschenheim, L. Noel, A. Orabona, B. Rhodine, M. Stangl, M. Young, E. Willems, and P. Winkle for field assistance. The study was funded by the Wyoming Game and Fish Department through support of the Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie.

LITERATURE CITED

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1975. Standard methods for the examination of water and wastewater. American Public Health Association, Washington, D.C.

BARICA, J., AND J. A. MATHIAS. 1979. Oxygen depletion and winterkill risk in small prairie lakes under extended ice cover. Journal of Fisheries Research Board of Canada 36: 980–986.

GREENBANK, J. 1945. Limnological conditions in ice covered lakes, especially as related to winterkill of fish. Ecological Monographs 15: 343–392.

HALSEY, T. G. 1968. Autumnal and over-winter limnology of three small eutrophic lakes with particular reference to experimental circulation and trout mortality. Journal of Fisheries Research Board of Canada 25: 81–99.

HINTZE, J. L. 1987. Number cruncher statistical software, version 5.01. NCSS, Kaysville, Utah.

MATHIAS, J. A., AND J. BARICA. 1980. Factors controlling oxygen depletion in ice-covered lakes. Canadian Journal of Fisheries and Aquatic Science 37: 185–194.

MILLER, A. I. 1989. Geomorphic controls on winterkill conditions in lakes of the Snowy Range, Wyoming. Unpublished master's thesis, University of Wyoming, Laramie.

NICKUM, J. G. 1970. Limnology of winterkill lakes in South Dakota. Pages 19–24 *in* E. Schneberger, ed., A Symposium on the Management of Midwestern Winterkill Lakes. Special publication of the North Central Division, American Fisheries Society, Bethesda, Maryland.

PATRIARCHE, M. H., AND J. W. MERNA. 1970. A resume of the winterkill problem. Pages 7–17 *in* E. Schneberger, ed., A Symposium on the Management of Midwestern Winterkill Lakes. Special publication of the North Central Division, American Fisheries Society, Bethesda, Maryland.

ZAR, Z. H. 1984. Biostatistical analyses, Prentice-Hall, Englewood Cliffs, New Jersey.

Received 22 June 1990
Revised 18 May 1991
Accepted 30 May 1991

Great Basin Naturalist 51(3), 1991, pp. 286–292

NONGAME WILDLIFE COMMUNITIES IN GRAZED AND UNGRAZED MONTANE RIPARIAN SITES

Terri Tucker Schulz[1,2] and Wayne C. Leininger[1]

Key words: birds, small mammals, Wilson's warbler, western jumping mouse, cattle grazing, Rocky Mountains, Colorado, riparian wildlife.

The riparian zone is an important habitat type for wildlife, providing numerous foraging and breeding sites (Thomas et al. 1979b). Greater numbers and diversity of nongame wildlife have been found in riparian areas when compared with upland habitats for birds in Colorado (Knopf 1985) and small mammals in Oregon (Cross 1985). Fifty percent of the nesting bird species in the Southwest (Johnson et al. 1977) and 82% of those in northern Colorado (Knopf 1985) occur in riparian habitats. The high density and species diversity of wildlife in riparian areas have been attributed to the many structural layers of riparian vegetation and to its ecotonal nature (Thomas et al. 1979a).

Livestock grazing can alter vegetative structure and composition of riparian habitat. Ryder (1980) stated that grazing, especially by livestock and big game, frequently changes plant species composition and growth form, density of stands, vigor and seed production of plants, and insect production. Bull and Skovlin (1982) attributed to livestock grazing the paucity of deciduous woody vegetation that was required by some bird species along Oregon streams. Annual livestock grazing depressed the numbers of all small mammal species observed at Malheur National Wildlife Refuge in Oregon (Cornely et al. 1983). Small mammal species richness and diversity was higher in 11-year-old exclosures in Nevada than in adjacent riparian areas grazed by cattle (Medin and Clary 1989).

This study was designed to determine the effects of season-long cattle grazing on nongame wildlife communities in a montane riparian zone in north central Colorado. Most research on the effects of livestock grazing on riparian bird communities has been conducted in the arid southwestern United States, and little is known about the effects of livestock grazing on birds or small mammals in more mesic environments.

STUDY AREA AND METHODS

This study was conducted within the riparian zone bordering Sheep Creek, 75 km northwest of Fort Collins, Colorado, in the Roosevelt National Forest, at approximately 2500 m elevation. Sheep Creek varies from 3 to 4 m in width, with a riparian zone 25–75 m wide.

According to USDA Forest Service records, the Sheep Creek Grazing Allotment received extremely heavy cattle grazing pressure until the 1950s. By the late 1940s, the entire riparian area was practically denuded, with little herbaceous plant cover and only a few remnant willow (*Salix* spp.) stumps remaining. The Forest Service and Colorado Division of Wildlife built two exclosures in the fall of 1956 to protect the riparian area from livestock overgrazing in an effort to improve the fisheries habitat. A third exclosure was constructed in the spring of 1959. The three exclosures protect a total of 40 ha of the riparian zone and 2.5 km of stream. Fences consisting of three-strand barbed wire were designed to restrict only livestock access to the riparian zone. Exclosures and grazed areas were interspersed along a 5-km section of Sheep Creek (Fig. 1).

---

[1] Range Science Department, Colorado State University, Fort Collins, Colorado 80523.

[2] Present address: Rocky Mountain Forest and Range Experiment Station, Forest Service, Fort Collins, Colorado 80526.

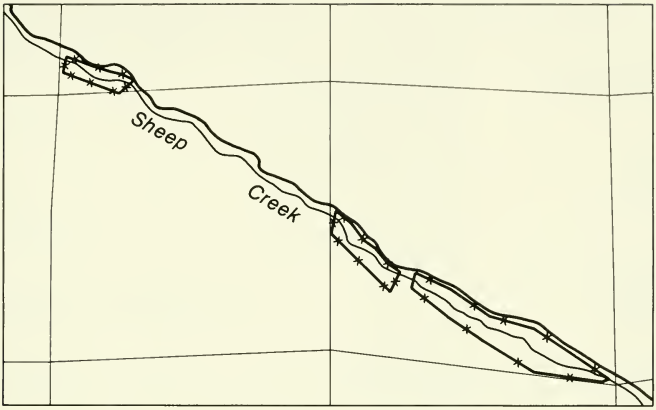


Fig. 1. Map of study area showing the Sheep Creek exclosures and adjacent grazed areas. Exclosures encompassing 40 ha of the riparian zone and 2.5 km of stream were constructed in the 1950s to protect the riparian area from overgrazing by domestic livestock. The Forest Service road that runs along the north side of the stream is shown on this map, as well as section lines for an indication of spatial scale (approximately 1 mi).

Stocking rates in the Sheep Creek Allotment have been reduced from nearly 1900 animal unit months (AUMs) in 1939 to 600 AUMs presently in the grazed area (unpublished data on file at USDA Forest Service). The allotment carrying capacity is estimated at 621 AUMs. Cattle graze the Sheep Creek Allotment season-long from approximately mid-June until mid-October. Utilization of forage by livestock was estimated from clipping vegetation at the end of the grazing season under protected cages and adjacent paired grazed plots. Cattle consumption of the current year's growth in the riparian area was 65% in both 1985 and 1986 (Schulz and Leininger 1990).

Streambank vegetation inside the exclosures is dominated by planeleaf willow (*Salix planifolia*), grasses and grasslike plants, including fowl bluegrass (*Poa palustris*), and rushes (*Juncus* spp.). Vegetation in grazed areas is composed predominantly of herbaceous species, including Kentucky bluegrass (*P. pratensis*), upland sedges (*Carex* spp.), beaked sedge (*C. rostrata*), white clover (*Trifolium repens*), and dandelion (*Taraxacum officinale*). In 1985 and 1986 total vascular vegetation cover, graminoid cover, and shrub cover in the exclosures were greater than in grazed areas (Schulz and Leininger 1990). The Sheep Creek exclosures had nearly twice the litter buildup, and willow canopy coverage was 8.5 times greater than in grazed areas (Schulz and Leininger 1990). Upland vegetation consists of ponderosa pine (*Pinus ponderosa*) with sparse understory on north-facing slopes and big sagebrush (*Artemisia tridentata*) on south-facing slopes. Aspen (*Populus tremuloides*) is also common in more mesic areas.

Strip transects for an index of bird abundance were conducted during May–June 1986 in the exclosures and adjacent grazed areas following methods described by Verner (1985). Transects were 20 m wide and 100 m long parallel to the stream channel. Transect width ensured that all observations fell within the riparian zone. Fourteen transects (7 within the grazed areas and 7 in the exclosures) were censused 10 times during the two-month period. Counts were made between 0630 and 1000 when birds are most active and vocal. Locations of birds were marked on data forms as we walked through the middle of each transect.

Twelve snap-trap transect lines for capturing small mammals were established parallel to the stream channel (6 inside exclosures and 6 in the grazed areas). Transect lines were 114 m in length with 20 stations, one every

TABLE 1. Total bird observations on 14 strip transects in grazed and ungrazed montane riparian sites May–June 1986.

Bird species	Scientific name	Grazed	Exclosures
American Robin	*Turdus migratorius*	35	15
Broad-tailed Hummingbird	*Selasphorus platycercus*	1	2
Brown-headed Cowbird	*Molothrus ater*	4	0
Cassin's Finch	*Carpodacus cassinii*	1	2
Chipping Sparrow	*Spizella passerina*	3	5
Clark's Nutcracker	*Nucifraga columbiana*	2	0
Dark-eyed Junco	*Junco hyemalis*	7	9
Empidonax Flycatcher	*Empidonax* spp.	3	2
House Wren	*Troglodytes aedon*	1	0
Killdeer	*Charadrius vociferus*	1	0
Lincoln's Sparrow	*Melospiza lincolnii*	4	13
MacGillivray's Warbler	*Oporonis tolmiei*	1	0
Mountain Chickadee	*Parus gambeli*	8	17
Mountain Bluebird	*Sialia currucoides*	2	0
Northern Flicker	*Colaptes auratus*	0	1
Pine Siskin	*Carduelis pinus*	1	0
Ruby-crowned Kinglet	*Regulus calendula*	8	8
Tree Swallow	*Tachycineta bicolor*	2	0
Warbling Vireo	*Vireo gilvus*	2	0
Western Tanager	*Piranga ludoviciana*	1	2
White-crowned Sparrow	*Zonotrichia leucophrys*	1	5
Wilson's Warbler	*Wilsonia pusilla*	0	9[a]
Yellow-bellied Sapsucker	*Sphyrapicus varius*	4	0
Yellow-rumped Warbler	*Dendroica coronata*	0	2
Number of individuals		92	92

[a] Difference between treatments was significant at the .05 level.

6 m, following Johnson (1982). The starting point of each transect line was randomly located between 10 and 20 m from the fenceline. Two Museum Special snap-traps were baited with peanut butter and set at each station. Traps were checked and reset every morning and evening at dusk. Transect lines were run for four days and nights in late July through August 1986 for a total of 1920 trap nights. Pitfall traps were also set for capturing shrews. Since trends in shrew abundance from pitfall traps were consistent with the snap-trap data, only snap-trap data is reported. All collected specimens were frozen and later identified by U.S. Fish and Wildlife Service museum personnel in Fort Collins. Shrews were identified following the key of Junge and Hoffmann (1981).

Paired *t* tests were used to compare total numbers of individuals of each bird and small mammal species by transect between grazed areas and exclosures. Homogeneity of variances was tested using Bartlett's test (Sokal and Rohlf 1981). Simpson's index of diversity (Simpson 1949) was calculated for exclosures and grazed areas using bird survey and small mammal snap-trap data. Since two communities can have the same index of diversity but have no species in common (Samson and Knopf 1982), Morisita's index of community overlap was also calculated. Morisita's index can be interpreted as the probability of randomly drawing two individuals from two populations (i.e., grazed areas and exclosures) that both belong to the same species, relative to the probability of randomly drawing two individuals of the same species from either of the populations alone (Horn 1966).

RESULTS

Twenty-one bird species were observed in the grazed transects, whereas 14 species were seen in the exclosures (Table 1). Eleven bird species were found in both areas. Total numbers of bird sightings were the same in both the grazed areas and the exclosures, with 92 observations. The American Robin (*Turdus migratorius*), with 35 sightings, was the most abundant species in the grazed areas, while the Mountain Chickadee (*Parus gambeli*), with 17 sightings, was the most common species in the exclosures (Table 1).

Wilson's Warbler (*Wilsonia pusilla*) was significantly more abundant ($P = .02$) in the exclosure transects. Lincoln's Sparrow

TABLE 2. Total small mammals captured with Museum Special snap-traps (number of trap nights = 1920) in grazed and ungrazed montane riparian sites July–August 1986.

Mammal species	Scientific name	Grazed	Exclosures
Deer mouse	*Peromyscus maniculatus*	15	1[a]
Golden-mantled ground squirrel	*Citellus lateralis*	1	0
Least chipmunk	*Eutamias minimus*	5	2
Longtail vole	*Microtus longicaudus*	0	1
Masked shrew	*Sorex cinereus*	4	5
Montane shrew	*S. monticolus*	1	9
Mountain vole	*M. montanus*	0	1
Northern pocket gopher	*Thomomys talpoides*	1	0
Western jumping mouse	*Zapus princeps*	1	22[b]
Total		28	41

[a] Differences between treatments were significant at the .05 level.
[b] Differences between treatments were significant at the .01 level.

(*Melospiza lincolnii*) ($P = .12$) also tended to be more abundant in the exclosures. Other species, e.g., Dark-eyed Junco (*Junco hyemalis*) and Ruby-crowned Kinglet (*Regulus calendula*), were equally common in grazed and ungrazed areas (Table 1).

Seven small mammal species were captured in the grazed areas, and an equal number were trapped in the exclosures (Table 2). Five small mammal species were common to both the grazed and ungrazed areas. Twenty-eight individual small mammals were trapped in the grazed area, compared with 41 in the exclosures (Table 2). The deer mouse (*Peromyscus maniculatus*), the most abundant small mammal species in the grazed area, was caught more often in the grazed areas than in the exclosures ($P = .04$). In contrast, the western jumping mouse (*Zapus princeps*), the most abundant species in the exclosures, was caught more often in the exclosures than in the grazed areas ($P = .006$) (Table 2). Other species such as the masked shrew (*Sorex cinereus*) appeared unaffected ($P > .25$) by cattle grazing (Table 2).

Simpson's diversity index for birds and small mammals was similar for the grazed areas and the exclosures (Table 3). Morisita's index of overlap was low for both taxa, based on the similarity of the communities in grazed areas and exclosures (Table 3).

TABLE 3. Comparison of nongame community parameters between grazed and ungrazed riparian sites.

Treatment	Species richness	Diversity index	Overlap
BIRD COMMUNITIES			
Grazed areas	21	0.83	15%
Exclosures	14	0.89	
SMALL MAMMAL COMMUNITIES			
Grazed areas	7	0.68	19%
Exclosures	7	0.66	

DISCUSSION

Breeding Birds

Bird species are differentially affected by cattle grazing in riparian areas. Mosconi and Hutto (1982) showed that some riparian bird species, such as American Robin, benefit from grazing, while others are negatively affected. Robins forage in short grassy areas (Bent 1949), which are more abundant in grazed areas along Sheep Creek than in the exclosures (Schulz and Leininger 1990).

Both Wilson's Warbler and Lincoln's Sparrow were common in ungrazed areas with abundant willows. Wilson's Warbler breeds in willow thickets along mountain streams (Bent 1953), while Lincoln's Sparrow prefers brushy vegetation with an understory of grasses and sedges (Bent 1968). The greater shrub coverage in the exclosures (Schulz and Leininger 1990) probably accounts for the observed differences in abundance of these two species. While small sample size is a concern in this study, other more extensive studies support these findings. In southeastern Wyoming, Lincoln's Sparrow and Wilson's Warbler dominate subalpine willow communities (Finch 1986).

Rucks (1978) stated that livestock grazing causes the replacement of shrub-nesting bird species with species showing no preference for vertical vegetation structure. Riparian areas dominated by planeleaf willow in southeastern Wyoming contain a unique, but depauperate, assemblage of bird species (Finch 1988). Our study supports the above findings. Wilson's Warbler and Lincoln's Sparrow appear to have been replaced by ubiquitous species such as American Robin in grazed areas along Sheep Creek.

Small Mammals

Patton (1977) stated that small rodents are probably the least understood and documented group of animals using the riparian habitat. Johnson (1982) felt that grazing increases the density of those small mammal species that require low levels of cover, while subsequently reducing the density of those requiring higher levels of cover. Our study agrees with earlier studies showing that the deer mouse is more abundant under grazed conditions (Black 1968, Johnson 1982).

In this study, the western jumping mouse was more abundant in the exclosures than in the grazed areas. According to Clark's (1971) study in western Wyoming, the western jumping mouse prefers moderately wet aspen and shrub-sedge savanna habitats within 100 m of water. This type habitat is more characteristic inside the exclosures than in grazed areas along Sheep Creek (Schulz and Leininger 1990). Our data support Cranford's (1983) suggestion that the quality and type of vegetation is more important in determining suitable habitat for the western jumping mouse than the availability of water.

While sampling only one year is a concern in this study, small mammal snap-trapping a second year would have sampled a replacement, not a stable, community. This replacement community may or may not have had the same species composition as the stable community.

Diversity Patterns

The three levels of diversity, within habitat, between habitat, and regional, are parameters used to describe wildlife communities. Within-habitat diversity refers to the number of species within an area of uniform vegetation structure (Noss 1983) such as the Sheep Creek exclosures. Between-habitat diversity reflects the differences seen between habitats such as the entire riparian zone (grazed and ungrazed areas combined). Regional diversity refers to the diversity across the landscape (Noss 1983).

Simpson's diversity index indicated similar levels of diversity in the nongame communities in grazed areas and exclosures. This measure of within-habitat diversity reflects the number and abundance of species populations within a habitat type (Samson and Knopf 1982). Morisita's index of overlap was quite low, suggesting that, although the nongame communities in grazed areas and exclosures have a similar level of diversity, they are quite different in species composition. This value indicates a high between-habitat diversity across the entire riparian zone. Livestock grazing appears to change habitat structure (Schulz and Leininger 1990), resulting in a shift in species composition of birds and small mammals in the montane riparian zone, while maintaining the level of diversity. Riparian areas that contain unique species such as Wilson's Warbler are important contributors to regional diversity of the forest.

Management Considerations

Riparian zones can be managed for nongame species richness by maintaining high structural diversity of vegetation. While the number of nongame species is important, managers should also use value judgments on the worth of individual species (Balda 1975). Thus, management should not maximize the numbers of two common species such as American Robin and Brown-headed Cowbird at the expense of one sensitive species such as Wilson's Warbler. Species such as Wilson's Warbler, Lincoln's Sparrow, and western jumping mouse that are sensitive to grazing pressure should be monitored as indicators of habitat change. Johnson (1982) pointed out the need to coordinate range and wildlife habitat management to ensure the existence of sensitive wildlife species that are negatively impacted by livestock grazing.

This study suggests that previous heavy cattle grazing changed the bird and small mammal community composition through reduction of shrub and herbaceous cover. More research should be done to determine the effects of different season-long intensities of grazing as well as different seasons of grazing on nongame wildlife communities.

ACKNOWLEDGMENTS

This research was funded by the Colorado State Agricultural Experiment Station, through Project No. 650, and the USDA Rangeland Research Grants Program. Cooperation of the Roosevelt National Forest in providing the study site and furnishing allotment data is appreciated. The authors wish to thank Drs. Eric Anderson, Deborah Finch, Curt Flather, R. Ryder, M. J. Trlica, and two anonymous reviewers for reviewing earlier versions of this manuscript.

LITERATURE CITED

BALDA, R. P. 1975. Vegetation structure and breeding bird diversity. Pages 59–80 *in* Symposium on Management of Forest and Range Habitats for Nongame Birds. USDA Forest Service General Technical Report WO-1.

BENT, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. Smithsonian Institute, U.S. National Museum Bulletin 196.

______. 1953. Life histories of North American wood warblers. Smithsonian Institute, U.S. National Museum Bulletin 203.

______. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Smithsonian Institute, U.S. National Museum Bulletin 237.

BLACK, H. L. 1968. Populations of small rodents in relation to grazing by cattle on foothills rangelands. Unpublished master's thesis, University of Utah, Salt Lake City.

BULL, E. L., AND J. M. SKOVLIN. 1982. Relationships between avifauna and streamside vegetation. Transactions of the Forty-seventh North American Wildlife and Natural Resources Conference 47: 496–506.

CLARK, T. W. 1971. Ecology of the western jumping mouse (*Zapus princeps*) in Grand Teton National Park, Wyoming. Northwest Science 45: 229–238.

CORNELY, J. E., C. M. BRITTON, AND F. A. SNEVA. 1983. Manipulation of flood meadow vegetation and observations on small mammal populations. Prairie Naturalist 15: 16–22.

CRANFORD, J. A. 1983. Ecological strategies of a small hibernator, the western jumping mouse, *Zapus princeps*. Canadian Journal of Zoology 61: 232–240.

CROSS, S. P. 1985. Responses of small mammals to forest perturbations. Pages 269–275 *in* Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service General Technical Report RM-120.

FINCH, D. M. 1986. Similarities in riparian bird communities among elevational zones in southeastern Wyoming. Pages 105–110 *in* Proceedings of the Wyoming Water 1986 and Streamside Zone Conference. University of Wyoming, Water Research Center, Laramie.

______. 1988. Bird-habitat relationships in subalpine riparian shrublands of the central Rocky Mountains. Pages 167–172 *in* Management of subalpine forests: building on 50 years of research. USDA Forest Service General Technical Report RM-149.

HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist 100: 419–424.

JOHNSON, R. R., L. T. HAIGHT, AND J. M. SIMPSON. 1977. Endangered species vs. endangered habitats: a concept. Pages 68–79 *in* Importance, preservation and management of riparian habitat. USDA Forest Service General Technical Report RM-43.

JOHNSON, S. J. 1982. Impacts of domestic livestock grazing on small mammals of forest grazing allotments in southwestern Idaho. Pages 242–250 *in* Wildlife-Livestock Relationships Symposium: Proceedings 10. University of Idaho, Moscow.

JUNGE, J. A., AND R. S. HOFFMANN. 1981. An annotated key to the long-tailed shrews (genus *Sorex*) of the United States and Canada, with notes on Middle American *Sorex*. Museum of Natural History, University of Kansas. Occasional Paper No. 94. 48 pp.

KNOPF, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105–111 *in* Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service General Technical Report RM-120.

MEDIN, D. E., AND W. P. CLARY. 1989. Small mammal populations in a grazed and ungrazed riparian habitat in Nevada. USDA Forest Service Research Paper INT-413.

MOSCONI, S. L., AND R. L. HUTTO. 1982. The effect of grazing on the land birds of a western Montana riparian habitat. Pages 221–233 *in* Wildlife-Livestock Relationships Symposium: Proceedings 10. University of Idaho, Moscow.

NOSS, R. F. 1983. A regional landscape approach to maintain diversity. Bioscience 33: 700–706.

PATTON, D. R. 1977. Riparian research needs. Pages 80–82 *in* Importance, preservation, and management of riparian habitats. USDA Forest Service General Technical Report RM-43.

RUCKS, J. A. 1978. Comparisons of riparian communities influenced by grazing. Pages 100–113 *in* Lowland River and Stream Habitat in Colorado: a Symposium. Colorado Wildlife Society and Audubon Council.

RYDER, R. A. 1980. Effects of grazing on bird habitats. Pages 51–66 *in* Management of western forests and grasslands for nongame birds. USDA Forest Service General Technical Report INT-86.

SAMSON, F. B., AND F. L. KNOPF. 1982. In search of a diversity ethic for wildlife management. Transactions of the Forty-seventh North American Wildlife and Natural Resources Conference 47: 421–431.

SCHULZ, T. T., AND W. C. LEININGER. 1990. Differences in riparian vegetation structure between grazed areas and exclosures. Journal of Range Management 43: 294–298.

SIMPSON, E. H. 1949. Measurement of diversity. Nature 16: 688.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2d ed. W. H. Freeman and Co., New York. 859 pp.

THOMAS, J. W., C. MASER, AND J. E. RODIEK. 1979a. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon, edges. USDA Forest Service General Technical Report PNW-85.

_____. 1979b. Wildlife habitats in managed rangelands—the Great Basin of southeastern Oregon, riparian zones. USDA Forest Service General Technical Report PNW-80.

VERNER, J 1985. Assessment of counting techniques. Current Ornithology 2: 247–302.

Received 20 December 1990
Revised 8 April 1991
Accepted 16 June 1991

Great Basin Naturalist 51(3), 1991, pp. 293–295

NEW RECORDS OF VASCULAR PLANTS ON THE LASAL MOUNTAINS, UTAH

W. Scott Richardson[1]

Key words: vascular plants, habitat, LaSal Mountains, Utah, Grand County, San Juan County, plant records.

The LaSal Mountains are an isolated mountain range in southeastern Utah ranging in elevation from 1690 m to 3914 m. This wide range in elevation and the accompanying variety of slopes and microhabitats result in an extremely diverse flora. The most recent description of the LaSal Mountain flora was made by M. A. Franklin (unpublished data, Brigham Young University, Provo, Utah) in the early 1980s. This list consisted of historic and recent collections of plants; at the present it represents the most complete floral listing of this area.

One aspect of a recent study on the LaSal Mountain black bear population (Frost 1990, Richardson 1991) was a description of their habitat requirements. This required, among other things, making a collection of plant specimens from a wide variety of communities. Much of the collecting occurred in remote areas with difficult accessibility. As a result, I collected 14 species of vascular plants not recorded by Franklin. Seven of these species are new county records, six from Grand County (*Lithospermum multiflorum, Silene scouleri, Chimaphila umbellata, Sorbus scopulina, Ribes hudsonianum, Osmorhiza occidentalis*), and one from San Juan County (*Chenopodium atrovirens*). Plant nomenclature follows Welsh et al. (1987).

APOCYNACEAE

Apocynum androsaemifolium L. var. *androsaemifolium*, Grand Co., UT, T26S, R25E, Sec. 5 NE 1/4, 2560 m, aspen community, 1 August 1989, S. Richardson 354 (BRY).

This was the only location on the mountain that I observed this species. Its presence in an aspen community was somewhat unusual because it generally is found in oak and maple habitats (Arnow et al. 1980).

BORAGINACEAE

Lithospermum multiflorum Torr., Grand Co., UT, T26S, R26E, Sec. 6 SW 1/4, 2439 m, ponderosa pine and Gambel oak community, 10 September 1988, S. Richardson 215 (BRY).

This is the first published record of this species in Grand County. It was found only in ponderosa pine communities on the extreme eastern portion of the mountain. Pretty stoneseed is easily identified by the presence of purple dye in the roots.

CAPRIFOLIACEAE

Lonicera utahensis Wats., Grand Co., UT, T26S, R24E, Sec. 1 NW 1/4, 2744 m, aspen and white fir community, 17 August 1988, S. Richardson 165B (BRY).

Grand Co., UT, T26S, R25E, Sec. 17 NW 1/4, 3049 m, aspen and conifer community, 2 June 1989, S. Richardson 285 (BRY).

I frequently found this species on the north end of the mountain at sites with high elevations and north-facing slopes. Its occupation of sites not easily accessible explains, perhaps, why it had not been collected earlier.

Sambucus caerulea Raf., Grand Co., UT, T26S, R24E, Sec. 31 NE 1/4, 2378 m, mountain brush community, 18 July 1988, S. Richardson 20 (BRY).

Blue elderberry is rare on the LaSal Mountains and, as far as I know, exists only at this location. Two large plants, approximately 3 m in height, are the extent of its known distribution on this mountain.

---

[1] Brigham Young University, Department of Zoology, Provo, Utah 84602.

CARYOPHYLLACEAE

Silene scouleri Hook., Grand Co., UT, T26S, R24E, Sec. 16 NE 1/4, 2805 m, aspen and conifer community, 30 June 1989, S. Richardson 336 (BRY).

San Juan Co., UT, T28S, R24E, Sec. 1 NW 1/4, 2744 m, Gambel oak and snowberry community, 4 August 1988, S. Richardson 103 (BRY).

Few specimens of this species have been collected in Utah (Welsh et al. 1987). The specimen (336) from Grand County represents a county record. It was not uncommon to find this species on the mountain. Both specimens were collected at elevations higher than what this species normally occupies (Welsh et al. 1987).

CHENOPODIACEAE

Chenopodium atrovirens Rydb., San Juan Co., UT, T28S, R25E, Sec. 18 SW 1/4, 2652 m, Gambel oak community, 29 June 1989, S. Richardson 328 (BRY).

Grand Co., UT, T26S, R24E, Sec. 28 SW 1/4, 2744 m, aspen and Gambel oak community, 4 August 1989, S. Richardson 363 (BRY).

Both specimens were collected on xeric sites in association with oak. Specimen 328 is the first of this species collected in San Juan County. These specimens lacked hastately lobed leaves and occupied higher elevation sites, distinguishing it from *C. fremontii*.

COMPOSITAE

Artemisia biennis Willd., Grand Co., UT, T26S, R24E, Sec. 29 SW 1/4, 2500 m, mountain brush community near a canal, 1 October 1988, S. Richardson 220 (BRY).

Grand Co., UT, T26S, R24E, Sec. 17 NW 1/4, 2561 m, aspen community near spring, 9 September 1989, S. Richardson 376 (BRY).

I found this species only on the north end of the mountain. Both specimens were found near water on disturbed sites, specimen 220 on a mudslide and specimen 376 in an area disturbed by livestock.

Chrysothamnus viscidiflorus (Hook.) Nutt. var. *viscidiflorus*, Grand Co., UT, T25S, R25E, Sec. 19 NE 1/4, 2439 m, Gambel oak community, 30 August 1989, S. Richardson 375 (BRY).

While *C. viscidiflorus* was common on the mountain, the variety *C. v.* var. *viscidiflorus* was found only at this location. The large leaves and glabrous stems and leaves separated it from the other varieties.

PYROLACEAE

Chimaphila umbellata (L.) Barton, Grand Co., UT, T26S, R24E, Sec. 17 SE 1/4, 2927 m, aspen and conifer community, 4 September 1988, S. Richardson 207 (BRY).

Grand Co., UT, T26S, R24E, Sec. 16 SW 1/4, 3049 m, conifer community, 30 June 1989, S. Richardson 338 (BRY).

This was a common species at high elevations on steep, north-facing slopes. These specimens represent the first pipsissewa collected in Grand County.

ROSACEAE

Geum alleppicum Jacq., Grand Co., UT, T26S, R25E, Sec. 4 NE 1/4, 2500 m, mountain brush community, 24 July 1989, S. Richardson 66, 67, 76, 77 (BRY).

Grand Co., UT, T26S, R25E, Sec. 17 NW 1/4, 2988 m, meadow in aspen community, 29 July 1988, S. Richardson 82 (BRY).

Few specimens of this species have been collected in Utah (Kaye Thorne, Brigham Young University Herbarium, personal communication), and these five specimens represent nearly half of the Utah material at the BYU Herbarium. This species was found only on the northeast portion of the mountain.

Sorbus scopulina Greene, Grand Co., UT, T26S, R24E, Sec. 1 NW 1/4, 2744 m, aspen and white fir community, 17 August 1988, S. Richardson 165C (BRY).

This is a rare species on the LaSal Mountains and was found only at two locations, both high-elevation, mesic sites on north-facing slopes. This specimen is the first recorded collection in Grand County.

SAXIFRAGACEAE

Ribes hudsonianum Richards., Grand Co., UT, T26S, R24E, Sec. 29 SW 1/4, 2500 m, mountain brush community, 1 October 1988, S. Richardson 227 (BRY).

This species was seen only once and is a new record for Grand County. Its location in a mountain brush community is somewhat unusual as its typical habitat is aspen or conifer (Welsh et al. 1987). The unarmed branches and large, strongly 3-lobed leaves helped distinguish this species.

UMBELLIFERAE

Osmorhiza occidentalis (Nutt.) Torr., Grand Co., UT, T26S, R24E, Sec. 7 SE 1/4, 2348 m, mountain brush community, 13 August 1988, S. Richardson 154 (BRY).

Grand Co., UT, T26S, R24E, Sec. 21 NW 1/4, 2988 m, aspen community, 3 June 1989, S. Richardson 289 (BRY).

Found only on the northwest corner of the mountain on mesic sites, this species is a new record for Grand County.

LILIACEAE

Allium biceptrum Wats., San Juan Co., UT, T27S, R25E, Sec. 6 SW 1/4, 3049 m, open meadow in aspen community, 5 August 1988, S. Richardson 129 (BRY).

This species is uncommon in San Juan County and is found mainly in the western half of the state (Welsh et al. 1987). This is one of the few alliums to occupy high elevations (Welsh et al. 1987).

ACKNOWLEDGMENTS

Dr. Stanley L. Welsh and Kaye H. Thorne of the Brigham Young University Herbarium provided critical assistance in identifying plant specimens. I thank them for their time and valuable assistance. I also thank C. L. Pritchett, H. L. Black, and S. L. Welsh for reviews of this manuscript. Funding was provided by Brigham Young University, Utah Division of Wildlife Resources, U.S. Forest Service, and private contributions.

LITERATURE CITED

Arnow, L., B. Albee, and A. Wyckoff. 1980. Flora of the central Wasatch front, Utah. University of Utah Printing Service, Salt Lake City, Utah. 663 pp.

Frost, H. C. 1990. Population and reproductive characteristics of black bears on an isolated mountain in southeastern Utah. Unpublished master's thesis, Brigham Young University, Provo, Utah. 50 pp.

Richardson, W. S. 1991. Habitat selection and feeding ecology of black bears in southeastern Utah. Unpublished master's thesis, Provo, Utah. 80 pp.

Welsh, S. L., N. D. Atwood, L. C. Higgins, and S. Goodrich. 1987. A Utah flora. Great Basin Naturalist Memoirs No. 9. 894 pp.

Received 19 June 1991
Accepted 1 September 1991

Great Basin Naturalist 51(3), 1991, pp. 296–299

CHECKLIST OF THE CULTIVATED TREES OF ST. GEORGE, WASHINGTON COUNTY, UTAH

Robert B. Warrick[1] and C. Frank Williams[2]

Key words: cultivated trees, checklist, Washington County, Utah.

The challenge by Welsh (1987) in the introduction to A Utah Flora provided the impetus for writing this paper. Welsh challenges future workers to focus more attention on the cultivated plants of the state, which are numerous but poorly represented in the herbaria.

Washington County, Utah, is the most botanically diverse county in the state, both in cultivated and noncultivated species. St. George is often described as the "Palm Springs" of Utah. Its climate is milder than any other portion of the state, and palm trees and other semitropical plants attest to this fact. For this reason, the diversity of trees growing in St. George is extensive.

The following checklist is the result of a two-month intensive inventory of the street trees of St. George, the county seat and largest city in Washington County. Because of the wide diversity of trees grown in St. George, the checklist does not include all cultivated trees of Washington County. However, the majority of the species that are cultivated in the county will be represented here.

Site Description

St. George is located in Zone 8a of the new USDA zone maps and rated at Zone 10 in the Western Garden Book system. The average annual minimum temperature is 9.5–12.2 C; average rainfall is 22.3 cm per year. The growing season averages 223 days per year, and extended periods of cold weather during the winter are rare (Eubank and Brough 1979).

The soils in St. George and Washington County in general are alkaline. The four soil types found within St. George include the Hantz and St. George silty clay loams, and the Junction and Tobler fine sandy loams (Mortensen et al. 1977).

Materials and Methods

The inventory was restricted to the "old city," as depicted on the 1956 revised plat of St. George. The surrounding communities of Bloomington, Bloomington Hills, Green Valley, Middleton, etc., were not part of the inventory, although a quick survey of these communities was conducted to search for species not encountered in St. George proper.

Each tree within the city right-of-way of the approximately 230 city blocks was mapped and the species, dbh (diameter at breast height), and percentage of live wood were determined. Trees with problems were also indicated. Noteworthy trees outside of the right-of-way were also mapped but designated as such. On such properties as city parks, the city cemetery, Red Hills Municipal Golf Course, and the campus of Dixie College, all trees were mapped.

Resources used to identify unknown trees include A Utah Flora (Welsh et al. 1987), Manual of Cultivated Plants (Bailey 1949), North American Trees (Preston 1976), Western Garden Book (Williamson 1979), and The Standard Cyclopedia of Horticulture (Bailey 1922). Local nurseries were also visited, but because many plants were mislabeled, all trees were double-checked against the abovementioned floras and field guides and with herbarium specimens at Brigham Young University. Many specimens were not available in the herbarium for comparison and collections were made and deposited at the BYU Herbarium for future workers.

---

[1] Coast Nurseries, 15914 Broadway, Gardena, California 90248.

[2] Department of Agronomy and Horticulture, Brigham Young University, Provo, Utah 84602.

Results and Discussion

Approximately 3000 city trees and ca. 500 other trees outside the city right-of-way were mapped. All trees on city property and right-of-ways were entered into a data base for future reference by city parks and recreation workers. The total number of species encountered was much higher than expected, with 130 taxa in 77 genera and 38 families noted.

The three most common street trees were *Morus alba* L. (white mulberry), 16.8%; *Fraxinus velutina* Torr. (velvet ash cultivars), 12.2%; and *Gleditsia triacanthos* L. (honey locust), 5.4%.

Thirty species previously unreported for the state were discovered; they are marked with an asterisk in the checklist. A few of these have been known by some to be growing in Utah or Washington County, but they have never been collected and preserved in herbaria or reported in the literature.

An annotated species list may be obtained from the authors.

Checklist of the Cultivated Trees of St. George, Washington County, Utah

Species preceded by an asterisk were either previously not known to be growing in the state of Utah or unreported in the literature and/or herbaria of the state.

Division Pinophyta

Cupressaceae

**Cupressocyparis leylandii* (Dallim & Jacks.) Dallim	Leyland cypress
Cupressus arizonica Greene	Arizona cypress
**Cupressus sempervirens* L.	Italian cypress
Juniperus chinensis L.	Chinese juniper
Juniperus chinensis L. 'Hollywood'	Hollywood juniper
Juniperus scopulorum Sarg.	Rocky Mountain juniper
Platycladus orientalis (L.)	Arborvitae, Chinese thuja

Cycadaceae

**Cycas revoluta* Thurb.	Sago palm, cycad

Ginkgoaceae

Ginkgo biloba L.	Ginkgo, maidenhair tree

Pinaceae

**Calocedrus decurrens* (Torr.) Florin	Incense cedar
Cedrus atlantica (Endl.) Manetti ex Carr	Atlas cedar
**Cedrus deodara* Loud.	Deodar cedar
Picea pungens Engelm.	Blue spruce
**Pinus halepensis* Mill.	Aleppo pine
**Pinus halepensis* Mill. var. *brutia* Henry	Mondell pine
Pinus monophyla Torr. & Frem.	Single-leaf pinyon
Pinus mugo Turra	Mugo pine, Swiss mountain pine
Pinus nigra Arnold	Austrian pine
**Pinus pinea* L.	Italian stone pine
**Pinus roxburghii* Sarg.	Chir pine, Indian longleaf pine
**Pinus thunbergiana* Parl	Japanese black pine

Podocarpaceae

**Podocarpus macrophylla* D. Don	Yew pine

Taxodiaceae

Sequoiadendron giganteum (Lindl.) Buech.	Sequoia

Division Magnoliophyta
Class Magnoliopsida

Aceraceae

Acer negundo L.	Box elder
Acer palmatum Thunb.	Japanese maple
Acer saccharinum L.	Silver maple

Anacardiaceae

Cotinus coggygria Scop.	Smoke tree
Pistacia atlantica Desf.	Mt. Atlas pistache
**Pistacia chinensis* Bunge	Chinese pistache
Pistacia vera L.	Pistacio
Rhus typhina L.	Staghorn sumac
Rhus typhina L. 'laciniata'	Fernleaf staghorn sumac

Aquifoliaceae

Ilex opaca Ait.	American holly

Betulaceae

Betula papyrifera Marshall	Paper birch
Betula pendula Roth	Weeping birch
Corylus avellana L. 'Contorta'	Harry Lauder's walking stick

Bignoniaceae

Catalpa speciosa Warder	Catalpa, Indian cigar tree
Chilopsis linearis (Cav.) Sweet	Desert willow

Ebenaceae

Diospyros sp.	Persimmon

Elaeagnaceae

Elaeagnus angustifolia L.	Russian olive

Fagaceae

Quercus pauciloba Rydb.	Wavyleaf live oak
Quercus turbinella Greene	Canyon live oak
Quercus spp.	Oak hybrids

Hamamelidaceae

Liquidambar styraciflua L.	Sweetgum

Hippocastanaceae

Aesculus hippocastanum L.	Horsechestnut

Juglandaceae

Carya illinoensis (Wangenh.) K. Koch	Pecan
Juglans nigra L.	Black walnut
Juglans regia L.	English walnut

Lauraceae

**Laurus nobilis* L.	Sweetbay

Leguminosae

Albizia julibrissin Durazz.	Mimosa, silk tree
Caesalpinia gilliesii (Wallich) Dietr.	Bird-of-paradise
Cercis canadensis L.	Redbud
Gleditsia triacanthos L.	Honey locust
Laburnum anagyroides Mebicus	Goldenchain
Parkinsonia aculeata L.	Paloverde
Prosopis glandulosa Torr.	Honey mesquite
Prosopis pubescens Benth.	Screwbean mesquite
**Robinia* x *ambigua* Poir. 'Idahoensis'	Idaho locust
Robinia pseudoacacia L.	Black locust
Sophora japonica L.	Japanese pagoda tree
Wisteria sp.	Wisteria

Lythraceae

Lagerstroemia indica L.	Crape myrtle (not crepe myrtle)

Magnoliaceae

Liriodendron tulipifera L.	Tulip tree, yellow poplar
**Magnolia grandiflora* L.	Southern magnolia
Magnolia soulangeana Soul.-Bod.	Showy magnolia

Malvaceae

Hibiscus syriacus L.	Rose-of-Sharon

Meliaceae

Melia azedarach L.	Texas umbrella, chinaberry tree

Moraceae

**Broussonetia papyrifera* L'Her.	Paper mulberry
Ficus carica L.	Fig
Maclura pomifera (Raf.) Schneider	Osage orange
Morus alba L.	White mulberry, fruitless mulberry
Morus nigra L.	Black mulberry

Myrtaceae

**Eucalyptus nicholii* Maiden & Blakely	Willowleaf eucalyptus
**Eucalyptus polyanthemos* Schauer	Silver dollar gum
**Feijoa sellowiana* Berg.	Pineapple guava

Oleaceae

Fraxinus excelsior L.	European ash
**Fraxinus oxycarpa* Willd. 'Raywood'	Raywood ash
Fraxinus velutina Torr.	Velvet ash
**Ligustrum lucidum* Ait.	Glossy privet
**Olea europea* L.	Olive

Platanaceae

Platanus x *acerifolia* Willd.	Sycamore, London plane tree
Platanus occidentalis L.	American sycamore
**Platanus racemosa* Nutt.	California sycamore

Rhamnaceae

Ziziphus jujuba Miller	Jujube

Rosaceae

Crataegus c.f. *laevigata* (Poir.) DC	English hawthorne
**Eriobotrya japonica* Lindl.	Loquat
**Eriobotrya deflexa* (Hemsl.) Nakai	Bronze loquat
Malus floribunda Sieb. ex Van Houtte	Flowering crabapple
Malus pumila Miller	Apple
Malus sp.	Crabapple
Photinia x *fraseri* Dress.	Photinia
Prunus armeniaca L.	Apricot
Prunus avium L.	Cherry
Prunus x *bleriana* Andre.	Flowering plum
**Prunus caroliniana* Ait.	Carolina laurel cherry
Prunus cerasifera Ehrh.	Flowering plum
Prunus cerasus L.	Pie cherry, sour cherry
Prunus domestica L.	Plum
Prunus dulcis (Miller) D. A. Webb	Almond
Pyrus calleryana Decne.	Bradford pear, Callery pear
Pyrus communis L.	Pear

Salicaceae

Populus alba L.	White poplar
Populus fremontii Wats.	Fremont poplar, Fremont cottonwood
Populus x *canadensis* Moench	Carolina poplar, cottonwood
Populus nigra L. var. *italica* Duroi	Lombardy poplar
Populus tremuloides Michx.	Quaking aspen
Salix babylonica L.	Weeping willow
Salix laevigata Bebb	Red willow
Salix matsudana Koidz.	Globe willow
Salix matsudana Koidz. 'Tortuosa'	Corkscrew willow

Sapindaceae

Koelreuteria paniculata Laxmann	Goldenrain tree
Sapindus saponaria L. var. *drummondii* (Hook. & Arn.) Benson	Soapberry

Simaroubaceae

Ailanthus altissima (Miller) Swingle	Tree-of-heaven

Tamaricaceae

Tamarix parviflora DC	Salt cedar, tamarisk

Tiliaceae

Tilia cordata L.	Small-leaved European linden
Tilia europea L.	European linden

Ulmaceae

Celtis occidentalis L.	Hackberry
Ulmus americana L.	American elm
Ulmus procera Salisb.	English elm
Ulmus pumila L.	Siberian elm

Verbenaceae

Vitex agnus-castus L.	Chaste tree

Division Magnoliophyta
Class Liliopsida

Agavaceae

Yucca brevifolia Engelm.	Joshua tree
Yucca sp.	

Palmaceae

**Chamaerops humilis* L.	Mediterranean fan palm
**Phoenix dactylifera* L.	Date palm
**Trachycarpus fortunei* Wendl.	Windmill palm
Washingtonia filifera (L. Linden) Wendl.	California fan palm
**Washingtonia robusta* Wendl.	Mexican fan palm

Literature Cited

Bailey, L. H. 1922. The standard cyclopedia of horticulture. 6 vols. MacMillan Co., New York.

_____. 1949. Manual of cultivated plants. Rev. ed. MacMillan Publishing Co., New York.

Eubank, M. E., and R. C. Brough. 1979. Utah weather. Horizon Publishers, Bountiful, Utah.

Mortensen, V. L., J. A. Carley, G. C. Crandall, K. M. Donaldson, G. W. Leishman. 1977. Soil survey of Washington County area, Utah. U.S. Department of Agriculture, Soil Conservation Service and U.S. Department of Interior, Bureau of Land Management, National Park Service, and Utah Agricultural Experiment Station. U.S. Government Printing Office.

Preston, R. J. 1976. North American trees. Iowa State University Press, Ames.

Welsh, S. L. 1987. Introduction. Pages 1–5 *in* S. L. Welsh, N. D. Atwood, L. C. Higgins, S. Goodrich, A Utah flora. Great Basin Naturalist Memoir No. 9. Brigham Young University Press, Provo, Utah.

Welsh, S. L., N. D. Atwood, L. C. Higgins, S. Goodrich. 1987. A Utah flora. Great Basin Naturalist Memoir No. 9. Brigham Young University Press, Provo, Utah. 894 pp.

Williamson, J. F., ed. 1979. The western garden book. Sunset Books, Lane Publishing Co., Menlo Park, California.

Received 5 January 1991
Revised 12 July 1991
Accepted 31 July 1991

INTERMOUNTAIN CONSORTIUM FOR ARIDLANDS RESEARCH

Intermountain Research Station, Shrub Sciences Laboratory
735 North 500 East, Provo, UT 84606
(801) 377-5717
Dr. E. Durant McArthur, President

INTERMOUNTAIN CONSORTIUM FOR ARIDLANDS RESEARCH FORMED

The first (organizational) meeting of the Intermountain Consortium for Aridlands Research (ICAR) was held in Salt Lake City on February 21, 1991. ICAR was established to promote, facilitate, and coordinate research and education on arid ecosystems in the Intermountain area. Charter institutions include these universities and federal and state agencies: Brigham Young University; Southern Utah University; University of Nevada–Reno; University of Utah; Utah State University; Wayne State University; Weber State University; Desert Research Institute; U.S. Department of the Interior, Bureau of Land Management, Utah State Office; U.S. Department of Agriculture, Forest Service, Intermountain Research Station; U.S. Department of the Interior, National Park Service, Great Basin National Park; and Utah Division of Wildlife Resources.

ICAR will

- promote research and education on aridland ecosystems
- facilitate interactions among aridlands scientists
- develop programs for educating the public on the ecological values and economic role of aridlands
- provide coordination between federal, state, and private agencies and institutions interested in Intermountain aridlands research and education
- identify high priority research needs in the Intermountain West arid zone
- identify research facilities and long-term data bases in the Intermountain West arid zone
- utilize the long-term research studies conducted at the Desert Experimental Range (87-square-mile area with 54 years of data) and elsewhere as a basis for development of research related to global change

Executive Committee

Durant McArthur, president
Intermountain Research Station

Kimball Harper, vice president
Brigham Young University

Bruce Freet, secretary-treasurer
Great Basin National Park

Neil West, board member
Utah State University

Ernest Eberhard, board member, Bureau of Land Management

Agencies and institutions with interest in aridland research and education are invited to contact the president for information about membership.

INFORMATION FOR AUTHORS

The *Great Basin Naturalist* welcomes previously unpublished manuscripts pertaining to the biological natural history of western North America. Preference will be given to concise manuscripts of up to 12,000 words.

SUBMIT MANUSCRIPTS to James R. Barnes, Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, Utah 84602. A cover letter accompanying the manuscript must include phone number(s) of the author submitting the manuscript; it must also provide information describing the extent to which data, text, or illustrations have been used in other papers or books that are published, in press, submitted, or soon to be submitted elsewhere. Authors should adhere to the following guidelines; manuscripts not so prepared may be returned for revision.

MANUSCRIPT PREPARATION. Consult Vol. 51, No. 2 of this journal for specific instructions on style and format. These instructions, GUIDELINES FOR MANUSCRIPTS SUBMITTED TO THE GREAT BASIN NATURALIST, supply greater detail than those presented here in condensed form. The guidelines are printed at the back of the issue; additional copies are available from the editor upon request. Also, check the most recent issue of the *Great Basin Naturalist* for changes and refer to the *CBE Style Manual*, 5th edition (Council of Biology Editors, One Illinois Center, Suite 200, 111 East Wacker Drive, Chicago, IL 60601-4298 USA, PHONE: (312) 616-0800, FAX: (312) 616-0226; $24).

TYPE AND DOUBLE SPACE all materials, including literature cited, table headings, and figure legends. Avoid hyphenated words at right-hand margins. Underline words to be printed in italics. Use standard bond (22 × 28 cm), leaving 2.5-cm margins on all sides.

SUBMIT 3 COPIES of the manuscript. Number all pages and assemble each copy separately: title page, abstract and key words, text, acknowledgments, literature cited, appendices, tables, figure legends, figures.

TITLE PAGE includes an informative title no longer than 15 words, names and addresses of authors, a running head of fewer than 40 letters and spaces, footnotes to indicate change of address and author to whom correspondence should be addressed if other than the first author.

ABSTRACT states the purpose, methods, results, and conclusions of the research. It is followed by 6–12 key words, listed in order of decreasing importance, to be used for indexing.

TEXT has centered main headings printed in all capital letters; second-level headings are centered in upper- and lowercase letters; third-level headings begin paragraphs.

VOUCHER SPECIMENS. Authors are encouraged to designate, properly prepare, label, and deposit high-quality voucher specimens and cultures documenting their research in an established permanent collection, and to cite the repository in publication.

REFERENCES IN THE TEXT are cited by author and date: e.g., Martin (1989) or (Martin 1989). Multiple citations should be separated by commas and listed in chronological order. Use " et al." after name of first author for citations having more than two authors.

ACKNOWLEDGMENTS, under a centered main heading, include special publication numbers when appropriate.

LITERATURE CITED, also under a centered main heading, lists references alphabetically in the following formats:

Mack, G. D., and L. D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. Journal of Wildlife Management 44: 695–700.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Coulson, R. N., and J. A. Witter. 1984, Forest entomology: ecology and management. John Wiley and Sons, Inc., New York. 669 pp.

TABLES are double spaced on separate sheets and designed to fit the width of either a single column or a page. Use lowercase letters to indicate footnotes.

PHOTOCOPIES OF FIGURES are submitted initially with the manuscript; editors may suggest changes. Lettering on figures should be large enough to withstand reduction to one- or two-column width. Originals must be no larger than 22 × 28 cm.

NOTES. If your manuscript would be more appropriate as a short communication or note, follow the above instructions but do not include an abstract.

A CHARGE of $45 per page is made for articles published; the rate for subscribers will be $40 per page. However, manuscripts with complex tables and/or numerous half-tones will be assessed an additional charge. Reprints may be purchased at the time of publication (an order form is sent with the proofs).

FINAL CHECK:

- Cover letter explains any duplication of information and provides phone number(s)
- 3 copies of the manuscript
- Conformity with instructions
- Photocopies of illustrations

(ISSN 0017-3614)

GREAT BASIN NATURALIST Vol. 51, No. 3, September 1991

CONTENTS

Articles

Habitat evaluation procedure for Rocky Mountain bighorn sheep in the Intermountain West. . . . . Tom S. Smith, Jerran T. Flinders, and David S. Winn **205**

Observations on the developmental biology of *Cicindela arenicola* Rumpp (Coleoptera: Cicindelidae) . . . . Karen Lyn Bauer **226**

Tree size and understory phytomass production in a western juniper woodland . . . . Milda R. Vaitkus and Lee E. Eddleman **236**

Physical characteristics of Blue Grouse winter use-trees and roost sites. . . . . Peter J. Pekins, Frederick G. Lindzey, and James A. Gessaman **244**

Habitat use and food selection of small mammals near a sagebrush/crested wheatgrass interface in southeastern Idaho . . . . David K. Koehler and Stanley H. Anderson **249**

Effects of convict cichlids on growth and recruitment of White River springfish . . . . Dallas Tippie, James E. Deacon, and Chih-Hsiang Ho **256**

Nest-site selection by Sage Thrashers in southeastern Idaho. . . . . Kenneth L. Petersen and Louis B. Best **261**

Fishes of Bly Tunnel, Lassen County, California . . . . Peter B. Moyle, Thomas Kennedy, Derek Kuda, Laurie Martin, and Gerold Grant **267**

Heavy metal tolerance of inland saltgrass (*Distichlis spicata*) . . . . R. A. Prodgers and W. P. Inskeep **271**

Notes

Notes on cryptogamic plants of Utah: range extensions and species new to the state from Capitol Reef National Park. . . . . John R. Spence **279**

Factors influencing dissolved oxygen concentrations during winter in small Wyoming reservoirs . . . . Paula M. Guenther and Wayne A. Hubert **282**

Nongame wildlife communities in grazed and ungrazed montane riparian sites . . . . Terri Tucker Shulz and Wayne C. Leininger **286**

New records of vascular plants on the LaSal Mountains, Utah . . . . W. Scott Richardson **293**

Checklist of the cultivated trees of St. George, Washington County, Utah . . . . Robert B. Warrick and C. Frank Williams **296**

MCZ
LIBRARY
FEB 06 1992
HARVARD
UNIVERSITY

THE GREAT BASIN NATURALIST

VOLUME 51 № 4 — DECEMBER 1991

BRIGHAM YOUNG UNIVERSITY

GREAT BASIN NATURALIST

Editor

James R. Barnes

290 MLBM
Brigham Young University
Provo, Utah 84602

Associate Editors

Michael A. Bowers
Blandy Experimental Farm
University of Virginia
Box 175
Boyce, Virginia 22620

Jeanne C. Chambers
USDA Forest Service Research
860 North 12th East
Logan, Utah 84322-8000

Jeffrey R. Johansen
Department of Biology
John Carroll University
Cleveland, Ohio 44118

Paul C. Marsh
Center for Environmental Studies
Arizona State University
Tempe, Arizona 85287

Brian A. Maurer
Department of Zoology
Brigham Young University
Provo, Utah 84602

Jimmie R. Parrish
BIO-WEST, Inc.
1063 West 1400 North
Logan, Utah 84321

Editorial Board. Richard W. Baumann, Chairman, Zoology; H. Duane Smith, Zoology; Clayton M. White, Zoology; Jerran T. Flinders, Botany and Range Science; William Hess, Botany and Range Science. All are at Brigham Young University. Ex Officio Editorial Board members include Clayton S. Huber, Dean, College of Biological and Agricultural Sciences; Norman A. Darais, University Editor, University Publications; James R. Barnes, Editor, *Great Basin Naturalist*.

The *Great Basin Naturalist*, founded in 1939, is published quarterly by Brigham Young University. Unpublished manuscripts that further our biological understanding of the Great Basin and surrounding areas in western North America are accepted for publication.

Subscriptions. Annual subscriptions to the *Great Basin Naturalist* for 1991 are $25 for individual subscribers, $15 for student and emeritus subscriptions, and $40 for institutions (outside the United States, $30, $20, and $45, respectively). The price of single issues is $12. All back issues are in print and available for sale. All matters pertaining to subscriptions, back issues, or other business should be directed to the Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, UT 84602.

Scholarly Exchanges. Libraries or other organizations interested in obtaining the *Great Basin Naturalist* through a continuing exchange of scholarly publications should contact the Exchange Librarian, Harold B. Lee Library, Brigham Young University, Provo, UT 84602.

EDITORIAL PRODUCTION STAFF

JoAnne Abel	Technical Editor
Carolyn Backman	Assistant to the Editor
Heidi Larsen	Production Assistant

Copyright © 1991 by Brigham Young University

Official publication date: 27 December 1991

ISSN 0017-3614
12-91 750 53847

The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 51 | 31 DECEMBER 1991 | NO. 4

Great Basin Naturalist 51(4), 1991, pp. 301–309

IMPACTS OF BLACK-TAILED PRAIRIE DOG RODENTICIDES ON NONTARGET PASSERINES

Anthony D. Apa[1,3], Daniel W. Uresk[2,4], and Raymond L. Linder[1]

ABSTRACT.—In 1983 zinc phosphide, strychnine with prebait, and strychnine without prebait were applied to black-tailed prairie dog (*Cynomys ludovicianus*) colonies in west central South Dakota. Short-term (four days later) and long-term (one year later) impacts of the rodenticides on Horned Larks (*Eremophila alpestris*) and other granivorous birds inhabiting prairie dog colonies were evaluated. Horned Larks and 49 other bird species were observed. Immediate impacts reduced Horned Lark relative densities 66% with strychnine only and 55% with prebaited strychnine. Zing phosphide caused no measurable reduction. Horned Larks showed no long-term direct impacts. Indirect negative impacts occurred through habitat changes following prairie dog control. The granivorous guild showed no short- or long-term effects.

Key words: Cynomys ludovicianus, Eremophila alpestris, *granivorous guild, zinc phosphide, strychnine.*

Poisons applied to oats are the past and present primary tool for black-tailed prairie dog (*Cynomys ludovicianus*) control. Strychnine was introduced into the United States about 1847, and its success as a rodenticide has varied (Crabtree 1962). The alkaloid form on grain was recommended by the U.S. Department of Agriculture at the beginning of the century (Merriam 1902, Crabtree 1962). Inconsistent treatment effects in certain situations and potential hazards to many nontarget species (Tietjen 1976) have caused concern.

Zinc phosphide was introduced as a vertebrate pest control agent in 1943 due to strychnine shortages during World War II (Crabtree 1962). Following replenished supplies of strychnine and the development of sodium monofluoracetate (Compound 1080), use of zinc phosphide as a field rodenticide was curtailed until it was developed specifically for black-tailed prairie dog control in 1976 (Tietjen 1976). Since 1976, zinc phosphide has been the only rodenticide available for prairie dog control when there is federal involvement.

Several granivorous passerines inhabit black-tailed prairie dog colonies (Agnew et al. 1986). Birds residing on prairie dog colonies that could suffer death or illness from poison consumption are those of seed-eating guilds (Root 1967, Creighton 1974.) This guild could consume treated grains. Tietjen (1976) observed Horned Larks (*Eremophila alpestris*) and Mourning Doves (*Zenaida macroura*) on zinc phosphide-treated prairie dog colonies, but observations after treatment did not locate any sick or dead birds. In contrast, Hegdal and Gatz (1977a) found significant mortality of nontarget seed-eating birds, especially Horned Larks and Mourning Doves, when strychnine-treated grain was applied to Richardson's ground squirrel (*Spermophilus richardsonii*) colonies. The U.S. Department of Interior (1956) acknowledged that nontarget losses occurred following exposure to strychnine and recommended that attempts be made to minimize the effects.

---

[1] South Dakota Cooperative Fish and Wildlife Research Unit, South Dakota State University, Brookings, South Dakota 57006.

[2] United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, South Dakota School of Mines, Rapid City, South Dakota 57701.

[3] Present address: Fish and Wildlife Resources, College of Forestry, Wildlife, and Range Sciences, University of Idaho, Moscow, Idaho 83843.

[4] Address all correspondence to Daniel W. Uresk at the address indicated.

Quantitative estimates that evaluate poison impacts on avian residents from prairie dog control have not been fully documented. The objectives of this study were to evaluate (1) short- and long-term effects of zinc phosphide (with prebait), strychnine with prebait, and strychnine without prebait on Horned Larks and the granivorous avian guild and (2) compare three rodenticide treatments. Immediate effects on birds by the three rodenticide treatments have been reported by Uresk et al. (1988).

STUDY AREA

The study area is located on Badlands National Park and Buffalo Gap National Grasslands in west central South Dakota. Climate is considered semiarid with an average annual precipitation of 40 cm at the Cedar Pass Visitors Center, Badlands National Park. Approximately 80% of the precipitation falls as thundershowers during April to September, and rainfall can be localized or cover large areas. Temperatures range from −5 C in January to 43 C in July, with an average annual temperature of 10 C.

Raymond and King (1976) described the soils on the area as sedimentary deposits of clay, silt, gravel, and volcanic ash. Topographic features consist of rugged pinnacles, vegetated table top buttes, creek gullies, and grassland basins. Gently rolling grasslands are located in the northern portion of the study area with elevation ranging from 700 to 1000 m.

The vegetation consists of a mosaic of native grasses, forbs, shrubs, and isolated trees. Dominant grasses include bluegrama (*Bouteloua gracilis*), buffalograss (*Buchloe dactyloides*), needleleaf sedge (*Carex eleocharis*), and western wheatgrass (*Agropyron smithii*). Common forbs include scarlet mallow (*Sphaeralcea coccinea*), American vetch (*Vicia americana*), dogweed (*Dyssodia papposa*), sage (*Salvia reflexa*), and prairie sunflower (*Helianthus petiolaris*). The dominant shrub species is pasture sagebrush (*Artemisia frigida*). Nonnative grasses include cheatgrass (*Bromus tectorum*) and Japanese chess (*B. japonicus*). (Scientific names of plants follow Nickerson et al. 1976 and Van Bruggen 1976.) Native herbivores are black-tailed prairie dog, mule deer (*Odocoileus hemionus*), Rocky Mountain bighorn sheep (*Ovis canadensis*), American bison (*Bison bison*), pronghorn (*Antilocapra americana*), black-tailed jackrabbit (*Lepus californicus*), and white-tailed jackrabbit (*L. townsendii*). Small rodents include deer mouse (*Peromyscus maniculatus*) and grasshopper mouse (*Onychomys leucogaster*). Livestock are not present in the Park, but bison graze all year. Cattle are allowed to graze the National Grasslands six months during the growing season each year.

METHODS

Eighteen sites on 15 prairie dog colonies were sampled in 1983 and 1984 with 9 treatment sites and 9 controls (Uresk et al. 1986). Sites were clustered into three major areas, and each rodenticide treatment had 3 treated and 3 control sites. Zinc phosphide with prebait was applied to the area within Badlands National Park because administrative restraints did not allow the use of strychnine. Four of the zinc phosphide (2 treatment and 2 control) sites were clustered and paired on a prairie dog colony of approximately 600 ha. The remaining treatment prairie dog colony was located northwest of the aforementioned larger colony, and the control colony was northeast of the larger colony in the Buffalo Gap National Grasslands. Strychnine with and without prebait treatment was randomly assigned to the two areas on the National Grasslands. The area with prebaited strychnine was located east and south of Scenic, South Dakota. All strychnine treatment and control sites were on isolated towns ranging from 12 to 283 ha. Within each treatment regime, treatment or control designation was determined randomly except when the National Park Service imposed administrative restrictions.

Avian populations were sampled on 18 permanent 805 × 62-m (4.9 ha) belt transects, one on each site. Relative densities of bird species were estimated using a modification of techniques developed by Emlen (1971, 1977) and Rotenberry (1982). The observer walked the transect line and counted birds up to 31 m on either side of the line. Sampling began one-half hour after sunrise and continued for approximately 4–5 hours; average walking time was 15–25 minutes per transect. Sampling was conducted on four consecutive days for each sampling session. Birds hovering over and/or flying over the transect were tallied. In 1983 four pretreatment sampling sessions, prior to poisoning prairie dogs, were conducted in June, July, August, and early September. The sampling session in early September occurred one week prior to poisoning. The first posttreatment session in late September commenced four days after treatment to evaluate short-term treatment effects. Four posttreatment sampling sessions were conducted in June, July, August, and September of 1984 to evaluate long-term treatment effects.

Bait Formulation and Application

Poison application was in accordance with federal label instructions. The untreated oats (prebait) and the poisoned oats were applied from 3-wheel drive ATVs fitted with bait dispensers (Schenbeck 1982). Smaller acreages were treated by hand using teaspoons (H. P. Tietjen, USFWS, Denver, Colorado, personal communication).

Prebait consisted of four grams of high-quality, untreated, steam-rolled oats applied at each prairie dog burrow. Three sites were prebaited on 20 September 1983 and three on 21 September 1983. A minimum of 95% of the burrows were prebaited. Prebait was applied (<0.01 m^2 area) at edges of prairie dog mounds. Three days after prebait application three sites were treated with 4 g of 2.0% active zinc phosphide steam-rolled oats. On 23 September 1983 three additional sites were treated with 8 g of 0.5% strychnine alkaloid steam-rolled oats per burrow. The last three sites were treated with strychnine oats on 24 September 1983 but were not prebaited.

Statistical Analyses

Analysis of covariance was used to compare each treated group (cluster) of sites with its respective control group. Applications of repeated measures were examined but required constant response through time; i.e., no interaction between time and treatment. These data did not show a constant response through time and had interactions; therefore we used covariance adjustments for individual posttreatment sampling sessions. Pretreatment observations were used as covariates. Effect of rodenticide treatment for each time point was estimated as the covariance-adjusted difference between treated and control sites for each rodenticide. After obtaining an overall rejection of the hypothesis of no treatment effect, contrasts for each rodenticide treatment compared to its control were evaluated for significance based on a variance estimated only from the sites in each cluster (variance was heterogeneous among clusters). If the correlation between pretreatment and posttreatment observations was not significant ($\alpha < 0.20$), then estimates of treatment effects were based on the difference between posttreatment and pretreatment observations (repeated measures). This analysis uses the interaction between time and treatment as the indicator of the significant change due to treatment (Green 1979). Rodenticides were compared by forming pairwise contrasts of the contrasts obtained for the individual rodenticide treatments. Randomization procedures (Edington 1980, Romesburg 1981) based on 10,000 random permutations of the data pairs among treatment groups were used to estimate statistical significance of the various contrasts. Variance of a contrast was calculated as the sum of the variances of the means in the contrast, with calculated individual variances based on the covariance and homogeneous variance assumptions appropriate for the particular variable.

Because omission of any effect due to poisoning was considered more serious than the potential incorrect declaration of a significant treatment effect, Type II error protection was produced by testing each contrast individually. However, some Type I error protection was afforded by testing individual contrasts only after first observing a significant ($P = .10$) overall test of treatment differences using analysis of covariance (Carmer and Swanson 1973). Individual contrasts were considered biologically significant at $P = .20$. Although admittedly unconventional, for the number of sites available for study, this significance criterion produces a power (probability of detecting a true difference) of approximately 0.80 for a contrast twice as large as its standard error. This was considered a reasonable

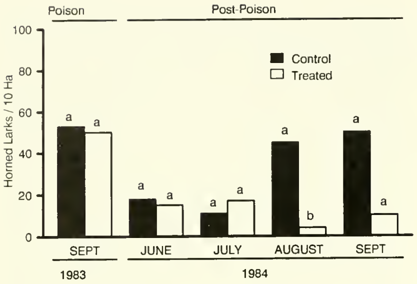


Fig. 1. Seasonal comparisons of Horned Lark relative densities on zinc phosphide–treated and control sites from initial treatment in September 1983 through September 1984. Adjusted means are from covariance analysis. Statistical analysis was conducted on posttreatment minus pretreatment. Means followed by the same letter by date are not significant at $\alpha = 0.20$ after F-protection at $\alpha = 0.10$.

combination of Type I and Type II error protection for this study (Carmer 1976).

RESULTS

Passerines

Forty-six species of birds were observed on all sites in 1983 and 40 in 1984. Eighteen bird species present on the sites were different between years. Total bird observations in 1983 were 8639; 65% of the sample consisted of Horned Larks, and 14% were Western Meadowlarks. However, in 1984 total bird observations were 5965, with Horned Larks accounting for 56% and Western Meadowlarks 18% of the sample. Unidentified species were less than 1% of the sample either year.

Horned Larks

There was no difference ($P = .977$) in the number of Horned Larks between treatment and control sites four days after application of zinc phosphide (Fig. 1). Relative densities of Horned Larks on the treatment sites were 50/10 ha, and control sites were 52/10 ha. No differences were found in relative densities between treated and control sites in June ($P = .479$) and July ($P = .486$) of 1984. The relative densities of Horned Larks in August 1984 were 93% higher (44/10 ha) on control sites than on treated sites (3/10 ha) ($P = .190$). In September 1984 similar trends were observed, but overall significant treatment effects were not evident ($P > .10$).

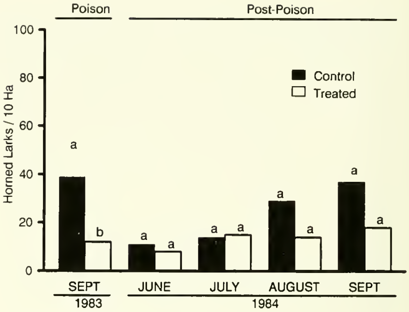


Fig. 2. Seasonal comparisons of Horned Lark relative densities on strychnine-treated and control sites from initial treatment in September 1983 through September 1984. Adjusted means are from covariance analysis. Statistical analysis was conducted on posttreatment minus pretreatment. Means followed by the same letter by date are not significant at $\alpha = 0.20$ after F-protection at $\alpha = 0.10$.

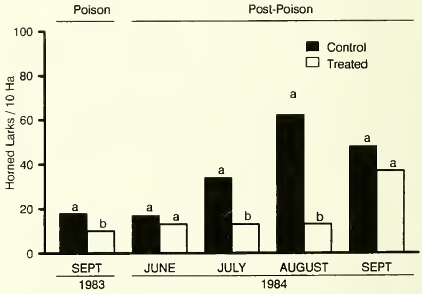


Fig. 3. Seasonal comparisons of Horned Lark densities on prebaited strychnine–treated and control sites from initial treatment in September 1983 through September 1984. Adjusted means are from covariance analysis. Statistical analysis was conducted on posttreatment minus pretreatment. Means followed by the same letter by date are not significant at $\alpha = 0.20$ after F-protection at $\alpha = 0.10$.

In 1983 Horned Lark densities were reduced 66% ($P = .109$; Fig. 2) on the strychnine only sites. No differences in relative densities for the Horned Lark occurred from June through September 1984 between treated and control sites ($P > .20$), indicating no long-term impacts.

Strychnine with prebait reduced Horned Lark relative densities 45% ($P = .128$; Fig. 3). By June 1984 Horned Lark densities were the

TABLE 1. Comparison of effects of zinc phosphide (ZnP) and strychnine (S-9) on Horned Lark relative densities/10 ha.

	Zinc phosphide versus strychnine			
	Adjusted effect			
Period	ZnP[a]	S-9[a]	Main effect[b]	Significance[c]
1983				
September	1 ± 19	−30 ± 19	31 ± 27	0.254
1984				
June	−5 ± 7	−4 ± 7	−1 ± 10	0.948
July	−6 ± 5	−2 ± 5	4 ± 7	0.717
August	−31 ± 3	3 ± 11	33 ± 11	0.183
September	−38 ± 20	−25 ± 20	−13 ± 28	NS[d]

[a] Effect adjusted through subtraction or analysis of covariance (mean ± standard error).

[b] Main effect calculated by difference of poisons.

[c] Probabilities calculated for contrasts in randomization test ($\alpha = 0.20$) based on variance heterogeneity after a significant F-protection at $\alpha = 0.10$ by analysis of variance or covariance.

[d] F-protection at $\alpha = 0.10$.

TABLE 2. Comparison of effects of zinc phosphide (ZnP) and prebaited strychnine (PS-9) on Horned Lark relative densities/10 ha.

	Zinc phosphide versus prebaited strychnine			
	Adjusted effect			
Period	ZnP[a]	PS-9[a]	Main effect[b]	Significance[c]
1983				
September	1 ± 19	−29 ± 19	30 ± 27	0.280
1984				
June	−5 ± 7	−2 ± 7	−2 ± 10	0.774
July	−6 ± 5	−20 ± 5	26 ± 7	0.020
August	−31 ± 3	−84 ± 11	53 ± 11	0.062
September	−38 ± 20	−32 ± 20	−6 ± 28	NS[d]

[a] Effect adjusted through subtraction or analysis of covariance (mean ± standard error).

[b] Main effect calculated by difference of poisons.

[c] Probabilities calculated for contrasts in randomization test ($\alpha = 0.20$) based on variance heterogeneity after a significant F-protection at $\alpha = 0.10$ by analysis of variance or covariance.

[d] F-protection at $\alpha = 0.10$.

same on treated and control sites ($P = .746$). In July 1984, 33 Horned Larks/10 ha were observed on the controls, while only 13/10 ha were on the treated sites ($P = .011$). In August relative densities of Horned Larks on control sites were 81% higher (62/10 ha) than on the treated sites (12/10 ha) ($P = .002$). By September 1984, however, there were no differences in relative densities between treated and control sites ($P > .10$).

Rodenticide Evaluation

The impact of zinc phosphide on Horned Larks was not different from that of strychnine only ($P = .254$; Table 1). In June and July 1984 there was no difference between the effects of zinc phosphide and strychnine on Horned Larks ($P = .948$ and $P = .717$, respectively). In August 1984 the effect of zinc phosphide was greater than that of strychnine ($P = .183$); however, in September 1984 no differences occurred between zinc phosphide and strychnine ($P < .10$).

A comparison of zinc phosphide and prebaited strychnine showed no differences in Horned Lark relative densities ($P = .280$) in September 1983 (Table 2). No differences were found between rodenticides in June 1984 ($P = .774$). During July and August 1984 differences were observed between zinc phosphide and prebaited strychnine ($P = .020$ and $P = .062$, respectively). Zinc phosphide showed less impact on Horned Lark densities than prebaited strychnine. However, in September 1984 no differences between zinc phosphide and strychnine were found ($P > .10$).

Strychnine only and prebaited strychnine were compared in September 1983, and no difference ($P = .964$) was found (Table 3). In June 1984 there was a difference of 2

TABLE 3. Comparison of effects of strychnine only (S-9) and prebaited strychnine (PS-9) on Horned Lark relative densities/10 ha.

	Strychnine versus prebaited strychnine			
	Adjusted effect			
Period	S-9[a]	PS-9[a]	Main effect[b]	Significance[c]
1983				
September	−30 ± 19	−29 ± 19	−1 ± 27	0.964
1984				
June	−4 ± 7	−2 ± 7	−2 ± 10	0.834
July	2 ± 5	−20 ± 5	22 ± 7	0.066
August	3 ± 11	−84 ± 11	87 ± 16	0.006
September	−25 ± 20	−32 ± 20	7 ± 28	NS[d]

[a] Effect adjusted through subtraction or analysis of covariance (mean ± standard error).

[b] Main effect calculated by difference of poisons.

[c] Probabilities calculated for contrasts in randomization test (α = 0.20) based on variance heterogeneity after a significant F-protection at α = 0.10 by analysis of variance or covariance.

[d] F-protection at α = 0.10.

TABLE 4. Bird species observed and included in the granivorous guild in 1983 and 1984 on all 18 study sites in west central South Dakota.

American Crow (*Corvus brachyrhynchos*)
American Goldfinch (*Carduelis tristis*)
American Robin (*Turdus migratorius*)
Black-billed Magpie (*Pica pica*)
Chestnut-collared Longspur (*Calcarius ornatus*)
Common Grackle (*Quiscalus quiscula*)
European Starling (*Sturnus vulgaris*)
Grasshopper Sparrow (*Ammodramus savannarum*)
Lark Bunting (*Calamorpiza melanocorys*)
Lark Sparrow (*Chondestes grammacus*)
Mourning Dove (*Zenadia macroura*)
Red-winged Blackbird (*Agelaius phoeniceus*)
Ring-necked Pheasant (*Phasianus colchicus*)
Rock Dove (*Columba livia*)
Savannah Sparrow (*Passerculus sandwichensis*)
Sharp-tailed Grouse (*Tympanuchus phasianellus*)
Vesper Sparrow (*Pooecetes gramineus*)
Western Meadowlark (*Sturnella neglecta*)

Horned Larks/10 ha between the two treatments ($P = .834$). Differences for these two treatments were observed in July (22 Horned Larks/10 ha) and August (87 Horned Larks/10 ha) 1984 ($P = .066$ and $P = .006$, respectively). Sites with prebaited strychnine showed the greatest reduction in Horned Lark relative densities. In September 1984 no differences in impacts between strychnine and prebaited strychnine were found ($P > .10$).

Granivorous Avian Guild

Seed-eating birds were combined into a guild because of small sample sizes (Table 4). In September 1983 no treatment effect ($P > .10$) was found on the seed-eating guild with Horned Larks excluded. This was also true for June ($P = .754$), July ($P = .300$), and September ($P = .841$) 1984.

In August 1984 seed-eating bird densities on the zinc phosphide-treated sites were similar ($P = .454$) to the controls. On the strychnine-treated sites 4 birds/10 ha were found, and even though 5 birds/10 ha were observed on the control sites, the means were significantly different ($P = .181$). The prebaited strychnine treatment means were also higher, with 20 birds/10 ha on the treated sites and 3 birds/10 ha on the controls ($P = .030$).

Rodenticide Evaluation

In August 1984 the effective difference of the prebaited strychnine treatment was larger than for the zinc phosphide (−30 birds/10 ha) ($P = .173$) and strychnine (−22) ($P = .011$) treatments (Table 5). Zinc phosphide and strychnine impacts on the seed-eating guild were similar (−8) ($P = .721$).

DISCUSSION

Bait Availability

More poisoned grain remained on the prairie dog mounds following poisoning with strychnine than with zinc phosphide (Apa et al. 1990). This phenomenon is most likely related to the "taste factor" that accompanies strychnine and zinc phosphide. Prairie dogs more readily consume zinc phosphide. Also, the time factor involved before a toxic reaction occurs after poison consumption (Crabtree 1962) could influence bait quantities remaining. The toxic reaction time is faster for strychnine than zinc phosphide; therefore, more

TABLE 5. Comparison of effects of zinc phosphide (ZnP) and strychnine only (S-9), zinc phosphide and prebaited strychnine (PS-9), and strychnine only and prebaited strychnine on seed-eating bird relative densities/10 ha.

	August 1984 Zinc phosphide versus Strychnine versus prebaited strychnine					
	ZnP	S-9	ZnP	PS-9	S-9	PS-9
Adjusted effect[a]	−18 ± 7	−10 ± 5	−18 ± 5	−12 ± 10	−10 ± 3	−12 ± 8
Main effect[b]	−8 ± 7		−30 ± 11		−22 ± 9	
Significance[c]	0.721		0.173		0.011	

[a] Effect adjusted through analysis of covariance (mean ± standard error).

[b] Main effect calculated by difference of poisons.

[c] Probabilities calculated for contrasts in randomization test (α 0.20) based on variance heterogeneity after significant F-protection at α 0.10 by analysis of covariance.

zinc phosphide could be consumed. These factors definitely affect availability of poisoned grain on prairie dog mounds following treatment.

Horned Larks

Treatments using zinc phosphide showed no direct impact on Horned Larks, but the two strychnine treatments did impact them. Strychnine is known for its avicidal efficacy (Courtsal 1983), but sparse documentation exists on its direct effects on birds. In this study, immediate direct losses were observed, and Horned Lark carcasses were found on the poisoned towns soon after poison application. Decreased relative densities of Horned Larks with both strychnine treatments were a result of direct poison toxicity and the large quantities of strychnine grain that remained on the mounds following posttreatment. The excess strychnine-treated grain was available to Horned Larks until bait disappeared or toxic effects were reduced. Hegdal and Gatz (1977a) found strychnine doses lethal to birds two months after poison application, resulting in significant reductions in Horned Lark populations in Wyoming.

There were no significant reductions in Horned Lark relative densities from zinc phosphide treatment because: (1) poison grain remaining was low, (2) birds have an aversion to black-colored foods (Rudd and Genelly 1956), and (3) birds have a negative sensory response to zinc phosphide (Siegfried 1968). Reduced impacts by zinc phosphide on birds have also been reported by Tietjen (1976), Tietjen and Matschke (1982), and Matschke et al. (1983). We believe zinc phosphide to be the preferred rodenticide for minimizing impacts on Horned Larks.

Indirect impacts on Horned Larks resulted from habitat changes. In 1984, when juveniles fledged, differences were observed between the control and treated sites. After the 1983 treatment of prairie dog colonies in the fall, Horned Larks nested on what appeared to be potential optimum habitat in spring 1984. Optimum nesting habitat consists of semibare or heavily grazed situations (Pickwell 1931, Dubois 1935, Bent 1968, Gietzentanner 1970, Creighton 1974). As summer progressed, prairie dogs were not available on treated sites to graze the spring growth. We observed many grasses (nonnative grasses and western wheatgrass) and forbs (prairie sunflower) that had obtained heights above the line of sight of ground-dwelling birds. Plant biomass increased and provided suitable habitat for Western Meadowlark, Lark Bunting, and Chestnut-collared Longspur (Giezentanner 1970).

In contrast, optimum habitat for Horned Larks was maintained by grazing of prairie dogs and other herbivores on the control sites throughout 1984. The low levels of prairie dog control achieved on the strychnine-treated towns (Apa et al. 1990) allowed surviving prairie dogs to consume vegetation and maintain optimum habitat for Horned Larks.

Granivorous Avian Guild

No immediate impacts on granivorous seed-eating birds were found, although we must acknowledge confounding individual effects that could influence results since we combined several granivorous species. Hegdal and Gatz (1977a) indicated that strychnine posed a threat to Red-winged, Yellow-headed (*Xanthocephalus xanthocephalus*), and Brewer's

(*Euphagus cyanocephalus*) Blackbirds; Vesper Sparrows; Western Meadowlarks; and Mourning Doves. Poisoned grains treated with zinc phosphide also posed a lesser threat to other seed-eating birds (Tietjen 1976, Hegdal and Gatz 1977b).

ACKNOWLEDGMENTS

Thanks are extended to Nebraska National Forest and Badlands National Park for providing study areas. Partial funding of this study was provided by National Agricultural Pesticide Impact Assessment Program (NAPIAP) and Nebraska National Forest (Interagency Agreement IAG-56).

LITERATURE CITED

Agnew, W., D. W. Uresk, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed grass prairie in western South Dakota. Journal of Range Management 39: 135–139.

Apa, A. D., D. W. Uresk, and R. L. Linder. 1990. Black-tailed prairie dog populations one year after treatment with rodenticides. Great Basin Naturalist 50: 107–113.

Bent, A. C. 1968. Life histories of North American flycatchers, larks, swallows, and their allies. Dover Publications Inc., New York.

Carmer, S. G. 1976. Optimal significance levels for application of significant difference in crop performance trials. Crop Science 16: 95–99.

Carmer, S. G., and M. R. Swanson. 1973. An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. Journal of American Statistics Association 68: 66–74.

Courtsal, F. R. 1983. Pigeons (Rock Doves). Pages E35–E41 *in* R. M. Timm, ed., Prevention and control of wildlife damage. Great Plains Agriculture Council Wildlife Resources Committee, Nebraska Cooperative Extension Service, Lincoln.

Crabtree, D. G. 1962. Review of current vertebrate pesticides. *In:* Vertebrate Pest Control Conference Proceedings, California Vertebrate Pest Control Tech, Sacramento. 390 pp.

Creighton, P. D. 1974. Habitat exploration by an avian ground-foraging guild. Unpublished dissertation, Colorado State University, Fort Collins.

DuBois, A. D. 1935. Nests of Horned Larks and Longspurs on a Montana prairie. Condor 37: 56–72.

Edington, E. S. 1980. Randomization tests. Marcel Dekker, Inc., New York. 287 pp.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk 88: 323–342.

———. 1977. Estimating breeding season bird densities from transect counts. Auk 94: 455–468.

Giezentanner, J. B. 1970. Avian distribution and population fluctuations on the shortgrass prairie of north central Colorado. Unpublished thesis, Colorado State University, Fort Collins.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley and Sons, New York. 257 pp.

Hegdal, P. L., and T. A. Gatz. 1977a. Hazards to seed-eating birds and other wildlife associated with surface strychnine baiting for Richardson's ground squirrels. EPA Final Report under Interagency Agreement EPA-IAG-D4-0449.

———. 1977b. Hazards to pheasants and cottontail rabbits associated with zinc phosphide baiting for microtine rodents in orchards. EPA Final Report under Interagency Agreement EPA-IAG-D4-0449.

Matschke, G. H., M. P. Marsh, and D. L. Otis. 1983. Efficacy of zinc phosphide broadcast baiting for controlling Richardson's ground squirrels on rangelands. Journal of Range Management 36: 504–506.

Merriam, C. H. 1902. The prairie dog of the Great Plains. Pages 257–270 *in* Yearbook of the United States Department of Agriculture. Government Printing Office, Washington, D.C.

Nickerson, M. F., G. E. Brink, and C. Fedema. 1976. Principal range plants of the central and southern Rocky Mountains: names and symbols. United States Department of Agriculture, Forest Service. General Technical Report RM-20, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. 121 pp.

Pickwell, G. A. 1931. The Prairie Horned Lark. Transactions of the Missouri Academy of Science (St. Louis) 27: 1–153.

Raymond, W. H., and R. U. King. 1976. Geological map of the Badlands National Monument and vicinity, west-central South Dakota. United States Geological Survey. Map I-934.

Romesburg, C. 1981. Randomization test. Resource Evaluation Newsletter. Pages 1–3. Technical Article 1. USDI-BLM, Denver Colorado.

Root, R. B. 1967. The niche exploitation pattern of the Blue-grey Gnatcatcher. Ecological Monographs 37: 317–349.

Rotenberry, J. T. 1982. Birds in shrubsteppe habitat. Pages 307–309 *in* D. E. Davis, ed., Handbook of census methods for terrestrial vertebrates. CRC Press, Inc., Boca Raton, Florida.

Rudd, R. L., and R. E. Genelly. 1956. Pesticides: their use and toxicity in relation to wildlife. California Fish and Game Bulletin No. 7.

Schenbeck, G. L. 1982. Management of black-tailed prairie dogs on the National Grasslands. Pages 207–217 *in* R. M. Timm and R. J. Johnson, eds., Fifth Great Plains Wildlife Damage Control Workshop Proceedings, 13–15 October 1981, University of Nebraska, Lincoln.

Siegfried, W. R. 1968. The reaction of certain birds to rodent baits treated with zinc phosphide. Ostrich 39: 197–198.

Tietjen, H. P. 1976. Zinc phosphide—its development as a control agent for black-tailed prairie dogs. United States Department of Interior, Fish and Wildlife Service Special Science Report Wildlife No. 195. 14 pp.

Tietjen, H. P., and G. H. Matschke. 1982. Aerial prebaiting for management of prairie dogs with zinc phosphide. Journal of Wildlife Management 46: 1108–1112.

URESK, D. W., R. M. KING, A. D. APA, AND R. L. LINDER. 1986. Efficacy of zinc phosphide and strychnine for black-tailed prairie dog control. Journal of Range Management 39: 298–299.

URESK, D. W., R. M. KING, A. D. APA, M. S. DEISCH, AND R. L. LINDER. 1988. Rodenticidal effects of zinc phosphide and strychnine on nontarget species. Pages 57–63 *in* D. W. Uresk, G. L. Schenbeck, and R. Cefkin, tech. coordinators, Eighth Great Plains Wildlife Damage Control Workshop Proceedings, Fort Collins, Colorado, GTR RM-154. USDA Forest Service Rocky Mountain Forest and Range Experiment Station.

USDI. 1956. Prairie dogs and their control. United States Department of the Interior, Fish and Wildlife Leaflet No. 357. 4 pp.

VAN BRUGGEN, T. 1976. The vascular plants of South Dakota. Iowa State University Press, Ames.

Received 1 May 1991
Accepted 15 September 1991

Great Basin Naturalist 51(4), 1991, pp. 310–315

MORPHOLOGICAL VARIABILITY AND CELL WALL COMPOSITION OF *PHAEODACTYLUM TRICORNUTUM* (BACILLARIOPHYCEAE)

Jeffrey R. Johansen[1]

ABSTRACT.—Five isolates of *Phaeodactylum tricornutum* Bohlin were examined in light and transmission electron microscopes. Although isolated from widely separated sites including both coastal marine and inland saline habitats, the morphology of the siliceous frustules of all isolates was very constant. The fusiform and triradiate forms, which have been reported as being non-siliceous in the past, were found to have an amorphous particulate nature in TEM. These forms were examined using EDAX SEM elemental analysis and were found to contain silica in their cell walls.

Key words: diatom, brackish-water; diatom, morphology; Great Salt Lake, Utah; Phaeodactylum; *Soap Lake, Washington.*

The diatom *Phaeodactylum tricornutum* Bohlin (1897) was first described from coastal marine waters in Sweden in 1897. Since then it has been observed in other marine coastal waters, particularly in areas of high enrichment. Rushforth et al. (1988) gave the first report of this species occurring in inland waters after discovering the taxon in phytoplankton samples from Farmington Bay, Great Salt Lake, Utah. *Phaeodactylum*, a monotypic genus, differs from other diatom genera in that it produces several types of cells, one bearing a weakly silicified naviculoid diatom valve, the others reportedly lacking siliceous valves and having either a fusiform, triradiate, or rarely cruciform shape (Wilson and Lucas 1942, Wilson 1946, Bourelly and Dragesco 1955, Borowitzka and Volcani 1978). The typically single-celled diatom can occasionally form chains of variable length (Borowitzka et al. 1977). The long and confused taxonomic history of this peculiar species has been covered elsewhere (Hendey 1954, Rushforth et al. 1988).

Subsequent to observation of *Phaeodactylum* populations in Great Salt Lake, I isolated the taxon from Soap Lake, Grant County, Washington, an unusual alkaline lake in the arid western part of the state. Originally, I thought my isolate was a small *Navicula* in the *Navicula saprophila/permitis/pelliculosa* complex. However, after careful electron microscope analysis I realized that it was indeed a *Phaeodactylum* species, although the alternate fusiform and triradiate cells have never been observed. I decided to undertake a comparative study of *Phaeodactylum* isolates to determine if morphological differences exist between marine and inland populations. This paper reports the results of that study.

METHODS

Five isolates of *P. tricornutum* were examined, all of which are maintained as part of the SERI Microalgae Culture Collection in Golden, Colorado. PHAEO1 (also designated TFX-1) was isolated from culture ponds at Woods Hole, Massachusetts, in September 1956 by Joyce and Ralph Lewin (Lewin et al. 1958). PHAEO2 (also designated BB) was isolated from coastal waters near Scripps Institution of Oceanography, La Jolla, California, by William H. Thomas (Barclay et al. 1986). PHAEO3 and PHAEO4 were isolated by myself from Farmington Bay, Great Salt Lake, Utah, 23 October 1986 and 26 March 1987, respectively. DIATO1 was isolated by myself from Soap Lake, Washington, 6 March 1987.

Marine isolates are routinely grown in GPM artificial seawater media, while inland strains are normally grown in SERI Type II/25 media (Barclay et al. 1986). However, all strains grow in SERI Type II/25. To eliminate morphological differences due to media differences, all cultures were grown in Type

---

[1] Department of Biology, John Carroll University, University Heights, Ohio 44118.

II/25 for one month prior to electron microscopical analysis.

P. tricornutum frustules are very fragile and are destroyed by boiling in nitric acid, a traditional diatom clearing procedure. To remove organic matter from the cultures, several techniques were employed, the best of which was to treat samples with concentrated H_2O_2 for 12–24 hours, followed by heating in a boiling water bath to degrade unreduced H_2O_2. Samples were then cleared of soluble salts by repeated washing and centrifugation. Cleared samples were mounted in Naphrax resin for light microscope analysis. It should be noted that this method was gentle enough that even the valves traditionally considered unsilicified were not dissolved. Diluted cleared samples were also mounted on formvar coated hexagonal copper grids for transmission electron microscopy (TEM). Grids were examined on a JEOL 100CX transmission electron microscope at an operating voltage of 80 kV. Additional cleared material was mounted on carbon stubs, carbon coated by vacuum evaporation, and examined with an EDAX 9100 attached to a Hitachi HHS-2R scanning electron microscope (SEM) at an operating voltage of 20 kV.

RESULTS

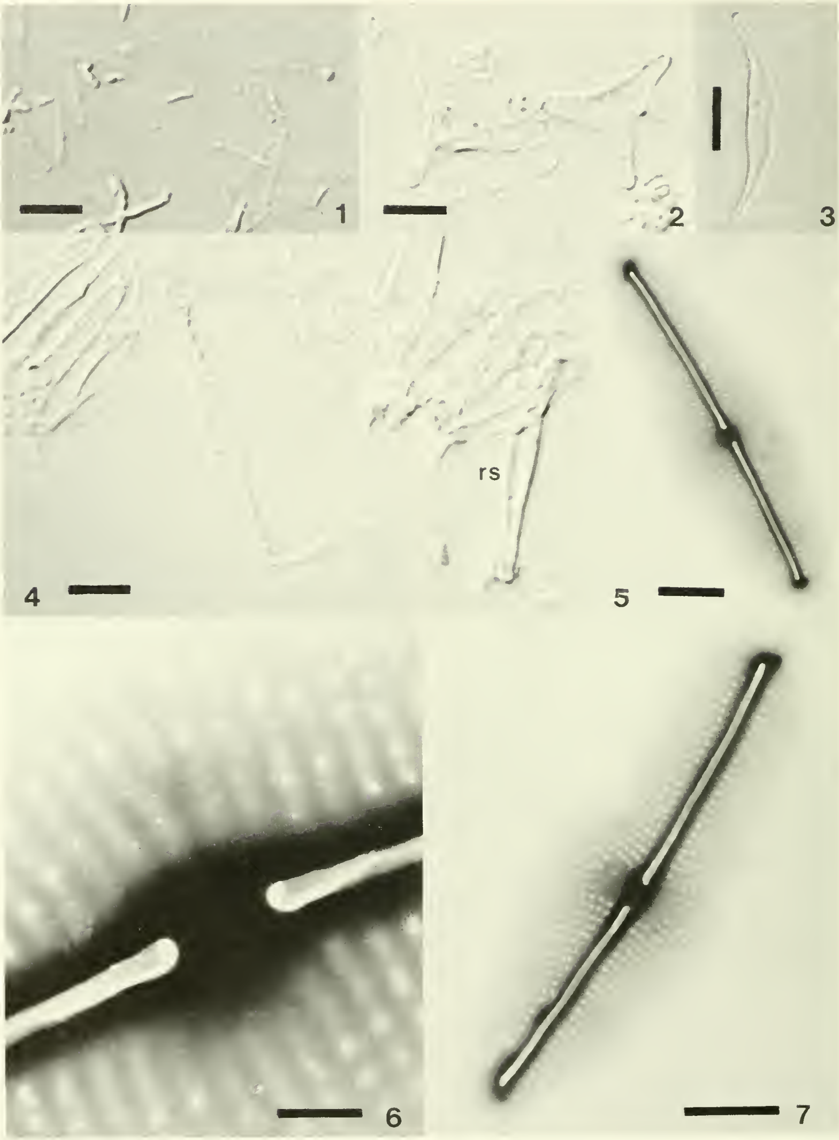
Simple elongated chloroplasts and circular lipid droplets are present in all cell types. In culture the naviculoid frustules produce more extracellular polysaccharides and form cohesive aggregates of cells that cannot be segregated by agitation. Fusiform and triradiate cells do not form cohesive aggregates. Naviculoid frustules were found in all five strains (Figs. 1, 5). Fusiform cells have been observed in PHAEO1, PHAEO2, PHAEO3, PHAEO4, and dominate cultures of PHAEO1 and PHAEO2 (Figs. 3, 4). During the past four years of culture history, triradiate cells have been observed only in PHAEO3 and PHAEO4, and they dominate cultures of those strains (Fig. 2). Chains like those recorded by Borowitzka et al. (1977) were seen rarely in cultures of PHAEO1 and PHAEO2.

Since naviculoid frustules were observed in all strains, morphological comparisons based on these cells can be made. Valves of all strains have overlapping dimensions and are morphologically indistinguishable. For this reason a summary of the traits of oval cells will be given without reference to strain. Cells are 7.5–16 μm long by 2.5–6.5 μm wide, with most cells 8–10 μm by 3–4.5 μm. The few larger cells were found in cultures of PHAEO1 dominated by the fusiform cells and may represent transitional forms between the two forms. In living material, two types of naviculoid cells were observed, long thin cells and cells of similar length but greater width. Wilson (1946) also observed these cell types and noted that the thinner cells are characteristic of rapidly growing cultures, whereas the larger cells are more typical of nutrient-deficient conditions.

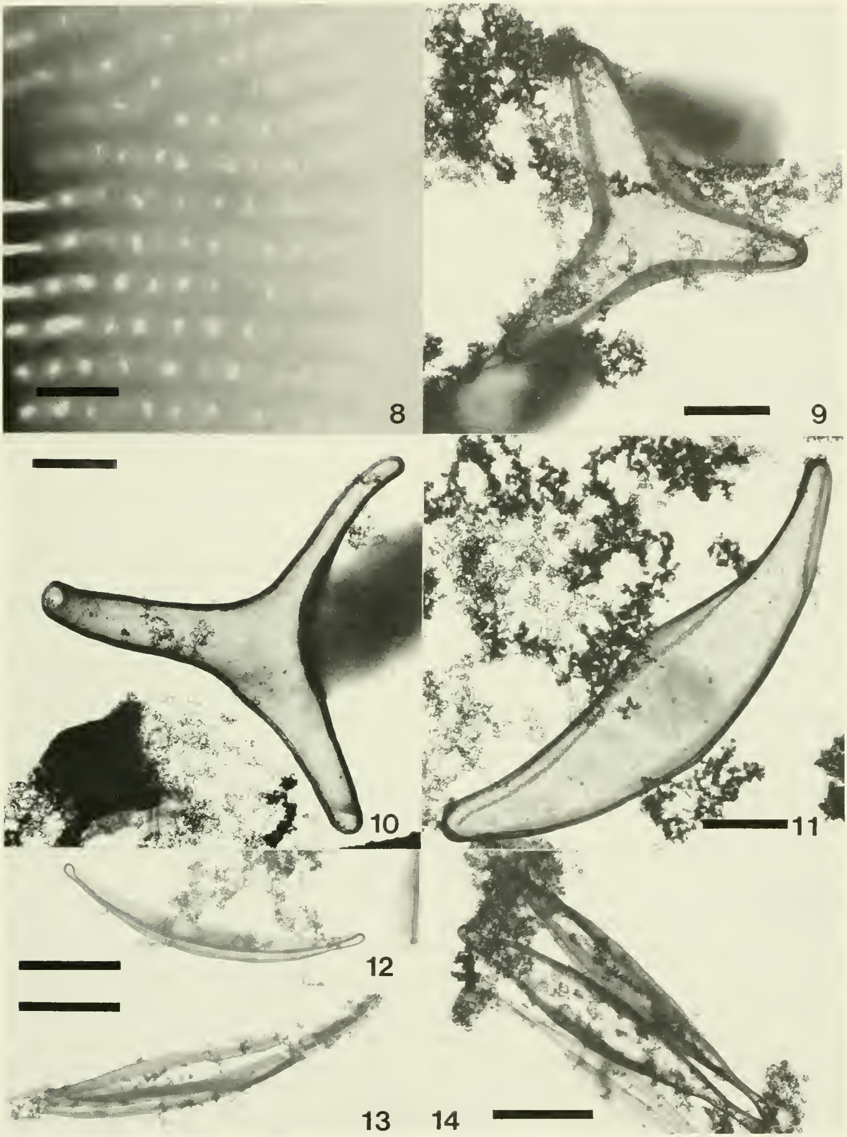
When naviculoid cells are cleared of organic matter, only the axial areas are distinguishable in light microscope mounts (Fig. 1). In TEM mounts, ultrastructure of the siliceous valve is revealed. Striae are usually parallel (Fig. 5), but they may be radiate (Fig. 7), especially around the central area (Figs. 6–8). Striae are evident as less thickly silicified areas of the valve that are perforated irregularly with simple pores (Figs. 5–8). Striae density ranges from 90 to 105 in 10 μm. The axial area is thickly silicified, wider at the center, and flexed to one side, giving the valves a slightly assymetrical aspect. The central area is further set off from the rest of the valve by having "ghost striae" not perforated by pores in an orbicular region around the center of the axial area (Figs. 5–6). The raphe is distinctly lateral, becoming filiform at both distal and proximal ends. Proximal raphe ends are hooked consistently toward the dorsal margin (Fig. 6).

Triradiate cells were common in the isolates from the Great Salt Lake (PHAEO3 and PHAEO4). The forms figured in this paper (Fig. 2) have shorter arms than those from the cultures first isolated (see Rushforth et al. 1988, Figs. 2, 3). The length of the arms as measured from valve center to tip ranges from 6 to 15 μm. In material cleared with hydrogen peroxide, the valve appears to be made of an amorphous particulate matrix and is clearly divided into valve face and mantle areas (Figs. 9, 10).

Fusiform cells are dominant in the marine isolates (PHAEO1 and PHAEO2). Cell dimensions are 15–27 μm long by 3–5 μm wide, dimensions similar to those reported by



Figs. 1–7. *Phaeodactylum tricornutum*, cleared specimens: 1, naviculoid valves of DIATO1 showing axial areas; 2, triradiate cells of PHAEO4; 3, dorsiventrally arched fusiform cell from PHAEO4 cultures; 4, fusiform cells of PHAEO2 (note the highly refractive specimen [rs] in the lower right, which is apparently more heavily silicified than other cells in the micrograph [scale 5 µm for Figs. 1–4]); 5–7, DIATO1 naviculoid cells showing morphology of the striae, raphe, and central area (scales 1 µm, 0.2 µm, and 1 µm, respectively).



Figs. 8–14. *Phaeodactylum tricornutum*, cleared specimens: 8, DIATO1 naviculoid valve showing details of striae ultrastructure (note irregular margin of the valve [scale = 0.2 μm]); 9, 10, PHAEO4 triradiate specimens showing amorphous particulate matrix of the valve (scale = 2 μm); 11, tumid dorsiventrally arched fusiform cell of PHAEO4 (scale = 2 μm); 12, PHAEO4; 13, PHAEO2 striated girdle bands; 14, PHAEO2 chain of cells showing striated girdle bands (scale = 5 μm for Figs. 12–14).

Wilson (1946), but shorter than those reported by Lewin (1958). Many fusiform valves have a distinctly dorsiventral appearance (Fig. 3), cells which are thought to be transitional between fusiform and triradiate cells (Borowitzka and Volcani 1978). In TEM the valves appear to be composed of the same particulate matrix as the triradiate cells (Fig. 11). The ultrastructure of these walls has been covered in detail elsewhere. They consist of an external corrugated layer subtended by a thicker fibrillar layer embedded in an amorphous matrix (Reimann and Volcani 1968, Borowitzka and Volcani 1978). All of these wall components have been assumed to be completely organic. Valve face and mantle regions are evident (Figs. 11, 12). The cingulum consists of a single siliceous striated band (Figs. 13, 14), which has been examined in detail elsewhere (Neuville et al. 1971, Borowitzka and Volcani 1978).

In cleared material some fusiform frustules appeared more refractive than others (Fig. 4). These cells had the appearance of having silica in their valves, even though previous workers reported that fusiform cell walls were unsilicified (Lewin 1958, Lewin et al. 1958, Borowitzka and Volcani 1978). In light of this finding, elemental analysis of cleared cell walls of cells grown in silica-deficient media was undertaken. The EDAX readout indicated the presence of silica, as well as smaller amounts of Na, Mg, Al, P, S, and Ca (Fig. 15).

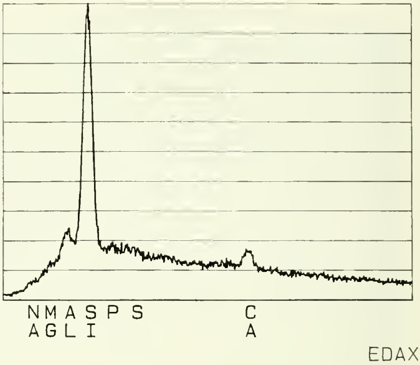


Fig. 15. EDAX elemental analysis of fusiform cell of *Phaeodactylum tricornutum*. Note the strong silica peak.

DISCUSSION

The morphological observations on inland and marine strains of *Phaeodactylum tricornutum* presented in this paper agree with the observations made by others (Wilson 1946, Lewin et al. 1958, Reimann and Volcani 1968, Borowitzka et al. 1977, Borowitzka and Volcani 1978). The inland strains did not differ morphologically from the marine strains. It is interesting to note that the Great Salt Lake strains were typically triradiate, the Soap Lake form produced only oval cells, and the marine forms were typically fusiform. However, given the past history of this species in culture (Wilson 1946), little significance can be attached to such differences.

External mucilaginous polysaccharides were associated only with oval cells, in agreement with the observations of Lewin et al. (1958). The ability of oval cells to grow on agar, the absence of mucilage from triradiate and fusiform cells, and the higher buoyancy of triradiate and fusiform cells suggest that the oval form is benthic, while the other forms are planktonic (Round et al. 1990). One wonders if in a small inland lake such as Soap Lake there is less opportunity for planktonic forms, and hence the dominance of the oval form.

By far the most surprising observation in this paper is the presence of silica in the cell walls of the fusiform and triradiate cells. Because this finding contradicted the assumptions of other workers, a number of valves were studied with EDAX elemental analysis. Care was taken to focus the beam on a very small region in the center of the valve to avoid picking up a silica signal from the siliceous bands. Lewin et al. (1958) reported the presence of flocculent, structureless silica following nitric acid digestion of fusiform cells. They assumed that the silica was from internal reserves, not from walls. Reimann and Volcani (1968) and Borowitzka and Volcani (1978) presented high-resolution TEM micrographs of the cell walls of *Phaeodactylum* fusiform cells. From examination of these micrographs, it seems possible that the fibrillar electron-dense layer of the wall may contain silica embedded in an organic matrix. Alternatively, silica may be present in some amorphous form. Since the silica is not organized into a solid siliceous structure as in other diatoms, it has been disregarded as a component of the walls, which have been falsely assumed to be totally organic.

It appears that silica is present to varying degrees within fusiform and triradiate cells (Fig. 4). The cultures in this study, routinely grown with fairly high available silica, were transferred to silica-free medium only a few days before analysis. It may be that others (Reimann and Volcani 1968, Borowitzka and Volcani 1978) have used low-silica media and thus not favored facultative silica deposition in fusiform and triradiate cells.

As this enigmatic and peculiar diatom continues to be found in new localities, it will probably continue to draw the interest of phycologists. It seems very possible that the taxon is widely distributed in inland saline water and has avoided detection because the cell walls tend to be destroyed in standard diatom preparation procedures.

LITERATURE CITED

BARCLAY, W., J. JOHANSEN, P. CHELF, N. NAGLE, P. ROESSLER, AND P. LEMKE. 1986. Microalgae culture collection 1986–1987. Solar Energy Research Institute, Golden, Colorado. 149 pp.

BOHLIN, K. 1987. Zur Morphologie und Biologie einzelliger Algen. Ofversigt af Kongliga Vetenskaps-Akademiens Forhhandligar 9:507–529.

BOROWITZKA, M. A., M. L. CHIAPPINO, AND B. E. VOLCANI. 1977. Ultrastructure of a chain-forming diatom *Phaeodactylum tricornutum*. Journal of Phycology 13:162–170.

BOROWITZKA, M. A., AND B. E. VOLCANI. 1978. The polymorphic diatom *Phaeodactylum tricornutum:* ultrastructure of its morphotypes. Journal of Phycology 14:10–21.

BOURELLY, P., AND J. DRAGESCO. 1955. Contribution a la connaissance d'une algue rarissime *Phaeodactylum tricornutum* Bohlin. Bulletin Microscopie Appliquee Series 2, 5(3,4):41–44.

HENDEY, N. I. 1954. Note on the Plymouth "Nitzschia" culture. Journal of the Marine Biological Association U.K. 33:335–339.

LEWIN, J. C. 1958. The taxonomic position of *Phaeodactylum tricornutum*. Journal of General Microbiology 18:427–432.

LEWIN, J. C., R. A. LEWIN, AND D. E. PHILPOTT. 1958. Observations on *Phaeodactylum tricornutum*. Journal of General Microbiology 18:418–426.

NEUVILLE, D., P. DASTE, AND L. GENEVES. 1971. Sur une souche axenique de *Phaeodactylum tricornutum* (Bohlin) isolee a partir d'une claire ostreicole de l'ile d'Oleron. Comptes Rendus Hebdomadaires des Seances. Academie des Sciences, Serie D 273:1221–1223.

REIMANN, B. E. F., AND B. E. VOLCANI. Studies on the biochemistry and fine structure of silica shell formation in diatoms. III. The structure of the cell wall of *Phaeodactylum tricornutum* Bohlin. Journal of Ultrastructure Research 21:182–193.

ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The diatoms, biology and morphology of the genera. Cambridge University Press, New York. 747 pp.

RUSHFORTH, S. R., J. R. JOHANSEN, AND D. L. SORENSEN. 1988. Occurence of *Phaeodactylum tricornutum* in the Great Salt Lake, Utah, USA. Great Basin Naturalist 48:324–326.

WILSON, D. P. 1946. The triradiate and other forms of *Nitzschia closterium* (Ehrenberg) Wm. Smith, forma *minutissima* of Allen and Nelson. Journal of the Marine Biological Association U.K. 26:235–270.

WILSON, D. P., AND C. E. LUCAS. 1942. *Nitzschia* cultures at Hull and Plymouth. Nature 149:331.

Received 12 February 1991
Revised 2 August 1991
Accepted 12 August 1991

Great Basin Naturalist 51(4), 1991, pp. 316–324

VEGETATION AND SOIL ZONATION ASSOCIATED WITH *JUNIPERUS PINCHOTII* SUDW. TREES

Guy R. McPherson[1], G. Allen Rasmussen[2], David B. Wester[3], and Robert A. Masters[4]

ABSTRACT.—Herbaceous vegetation pattern and soil properties around individual *Juniperus pinchotii* Sudw. trees were studied on a grazed and a relict grassland in western Texas. Herb standing crop and soil samples were obtained under the canopy, at canopy edge, and beyond the canopy edge of three to five trees on each of four dates. Standing crop was lowest midway between the bole and canopy edge. Soil organic matter was highest under juniper canopies on both sites. Soil pH and P were not related to distance from tree bole on either site. Herbaceous pattern from under the canopy to canopy edge apparently depended primarily on individual tree size. However, trees had little influence on herbaceous vegetation pattern 3–5 m beyond canopy edge, a response attributed to distance-independent interaction between *J. pinchotii* and herbaceous vegetation. Given a shallow soil underlain by indurated caliche and tree densities ranging from 288 (relict size) to 2123 (grazed site) trees/ha, the interaction between *J. pinchotii* and herbaceous vegetation did not change over a distance of 3–5 m from tree canopy edge in our study area.

Key words: Juniperus pinchotii, *redberry juniper, vegetation pattern, soil nutrients, herbivory, relic area, competition.*

Zones of herbaceous vegetation around *Juniperus* trees have been reported for several species in the western United States (Arnold 1964, Clary 1973, Springfield 1976, Everett et al. 1983, Schott and Pieper 1985). The most commonly recognized vegetation zones are: (1) under woody plant canopies, where *Juniperus* litter and shade alter microenvironment; (2) in a transition zone, where *Juniperus* roots compete with herbaceous plants for water and nutrients; and (3) in the interstice between trees, where trees do not influence herbaceous vegetation. In contrast, a zonation pattern was not detected around *J. virginiana* in Oklahoma (Engle et al. 1987) or *J. monosperma* in New Mexico (Armentrout and Pieper 1988). In these studies, herbaceous vegetation beyond tree canopies did not change with increased distance from trees.

Woody species influence soil properties primarily by rooting and litterfall characteristics (Barth 1980). Chemical constituents from surrounding soil are taken up by tree roots and concentrated in biomass. Litterfall transfers much of this biomass to the area beneath the canopy where it accumulates, and decomposition releases chemical constituents to the underlying soil. Soluble salts (Fireman and Hayward 1952, Sharma and Tongway 1973), nitrogen and phosphorus (reviewed by Tiedemann 1987), and zinc, iron, and magnesium (Hibbard 1940, Follett 1969, Barth 1980) have been implicated in this process.

Juniperus pinchotii Sudw. (nomenclature follows Correll and Johnston 1970), a sprouting evergreen conifer commonly found on limestone or gypseous soils, occupies about 2.4 million ha of rangeland in western and central Texas (Adams 1972). Throughout its range, *J. pinchotii* migrated quickly onto prairies during the expansion of the cattle industry (1870–1920) (Hall and Carr 1968, Adams 1975). Western Texas populations of *J. pinchotii* previously restricted to buttes and escarpments have subsequently expanded into adjacent grasslands and have become a major vegetation component (Ellis and Schuster 1968). The primary objective of this study was to determine the effects of individual *Juniperus pinchotii* trees on herbaceous vegetation and soil properties at a grazed and a relict site in western Texas.

STUDY AREAS

Two western Texas study sites were used.

---

[1] Forest-Watershed Sciences Program, School of Renewable Natural Resources, 325 Biological Sciences East, University of Arizona, Tucson, Arizona 85721.
[2] Range Science Department, Utah State University, 4 UMC 5230, Logan, Utah 94322.
[3] Department of Range and Wildlife Management, Texas Tech University, Lubbock, Texas 79409.
[4] 362F Plant Science Building, University of Nebraska, East Campus, Lincoln, Nebraska 68583.

Flattop Mountain, an isolated butte 11 km northwest of Snyder (101°10′W, 33°00′N), has not been grazed by livestock but is accessible to wildlife species and supports relict vegetation (McPherson 1987). Nine km southeast of the butte is an area with considerable historic grazing pressure. The grazed site is contiguous with the Llano Estacado High Plains; the relict site is a High Plains outlier (Brown and Schuster 1969). Average annual precipitation is 472 mm (Dixon 1975). Dominant soil on both sites is a shallow (about 50 cm) clay loam of the Lea-Slaughter complex (fine-loamy, mixed, thermic Petrocalcic Paleustolls and clayey, mixed, thermic, shallow Petrocalcic Paleustolls) (Dixon et al. 1973, Dixon 1975). These sites represent environmental settings whose primary extrinsic difference is domestic livestock grazing. The sites may also have intrinsic soil differences.

METHODS

On each site, 20 *Juniperus* plants were selected randomly, except for the requirements that they were (1) beyond the shading influence of other junipers; (2) between 1.0 and 4.0 m tall; and (3) at least 5 m from roads, shallow soil (gravel present at surface), or visibly disturbed areas. Standing crop of herbaceous vegetation was estimated around three to five randomly selected trees on each site in July (corresponding to peak standing crop) and October (to assess autumn productivity) 1984 and 1985, years in which study sites received 42 and 96% of long-term growing season precipitation (420 mm), respectively (McPherson 1987). Transects were established in the cardinal directions from the stem, ending 3 m beyond the canopy edge. Rectangular quadrats (0.10 m^2) were located at midpoint between canopy edge and stem (location 1), at canopy edge (location 2), and at 1.0-m intervals beyond the canopy edge (locations 3–5). Two quadrats were randomly located along each of 10 randomly located 5-m permanent transects in the interstice between trees (at least 5 m from nearest *Juniperus* plant; location I). Standing crop in quadrats was harvested to a 2.5-cm stubble height and separated by species. Herbage samples were oven-dried at 60 C for 48 h and weighed.

Two complete soil horizons were exposed and profiles described to the depth of indurated caliche on each site (McPherson 1987). Soil samples were collected from the 0–10-cm soil layer halfway between bole and canopy edge, at canopy edge, and at 1, 2, and 3 m along a southward transect from five randomly selected trees on each site in May 1986. Determination of calcium carbonate equivalent followed Richards (1954); organic matter content (OM) was determined by wet digestion (Prince 1955). Samples were analyzed for nitrogen (N), potassium (K), phosphorus (P), exchangeable calcium (Ca), sodium (Na), and magnesium (Mg) following Onken et al. (1980). Soluble salt and pH determination followed McLean (1982).

Species occurring with less than 5% frequency on all sites and dates were removed from the data set (Gauch 1982), leaving 57 species for subsequent analyses. Standing crop values were log transformed (Steel and Torrie 1980). Analysis of variance, Fisher's protected LSD, and reciprocal averaging ordination (RA) were used to analyze the effect of *Juniperus* trees on herbaceous vegetation and soil properties. Variability from tree to tree was taken into account by considering trees as blocks in a randomized complete block design in the analysis of variance. The "treatment effect" in this analysis was quadrat distance from tree bole.

RESULTS

Herbaceous Vegetation

Strong interactions ($P < .01$) between tree (block) and quadrat distance from tree (treatment) were exhibited by 56 of 57 species on all dates and sites (a tree-×-distance interaction was not present [$P > .05$] for *Bouteloua curtipendula* [Michx.] Torr. on the relict site on any date). Tree-×-distance interactions were also exhibited by plant guilds (cool-season grasses, warm-season grasses, forbs) and for total standing crop.

With only one grazed site and one relict site, it is not possible to statistically test the effect of site. Within a site, apparent differences in aboveground biomass between years (Table 1) were attributable to differences in precipitation (about twice as great in 1985 as 1984). (For elaboration of site and year effects on herbaceous production, see McPherson and Wright 1990.) However, vegetation composition within each site was similar on all sampling dates (Table 1). Ordination results

TABLE 1. Standing crop (g/m^2) of selected herbaceous species on grazed and relict grassland at six locations around *Juniperus pinchotii* trees in western Texas, July and October 1984 and 1985 (each number is mean of four cardinal directions and three to five trees).

Species[1]	GRAZED SITE											
	July 1984						October 1984					
	Location[2]						Location					
	1	2	3	4	5	1	1	2	3	4	5	1
GRASSES												
ARSP	0	6	90	192	173	270	0	401	125	113	124	156
BOCU	6	29	24	193	16	23	0	141	107	38	63	53
BUDA	0	2	4	2	2	6	0	6	4	6	6	5
TRMU	0	2	6	58	4	34	0	72	24	61	64	52
STNE	121	61	0	0	0	0	0	0	0	0	0	0
SIHY	0	11	0	0	0	0	70	0	0	0	0	0
Other grasses	2	13	4	10	6	15	0	122	46	57	60	27
FORBS												
CRDI	0	0	2	20	51	98	0	37	111	73	96	80
SICA	8	28	0	0	0	0	146	0	11	158	0	6
ZIGR	0	4	2	24	2	39	12	60	12	7	13	65
EVNU	0	4	17	34	8	43	0	8	15	21	27	30
LEER	0	0	37	2	6	14	0	2	8	2	0	23
CADR	0	4	6	6	4	8	2	11	6	38	63	37
ERMO	0	0	0	0	0	0	0	0	0	0	0	0
Other forbs	71	94	96	139	120	149	16	126	99	98	276	158
TOTAL	208	258	288	680	392	699	246	986	568	672	792	692
	RELICT SITE											
GRASSES												
ARSP	0	2	2	161	73	113	0	4	0	4	0	52
BOCU	248	217	436	285	333	830	26	116	157	95	122	184
BUDA	0	2	14	23	15	18	0	8	2	0	2	0
TRMU	0	13	25	19	0	60	0	42	0	19	22	30
STNE	123	19	13	0	0	0	0	0	0	34	0	39
SIHY	0	0	0	0	0	0	62	7	0	0	0	0
Other grasses	56	155	59	171	2	82	8	120	156	107	59	31
FORBS												
CRDI	0	0	0	0	0	0	0	0	0	0	0	0
SICA	6	0	0	0	0	0	30	2	0	0	20	5
ZIGR	0	0	0	0	0	0	0	0	0	0	0	0
EVNU	0	0	0	0	6	0	0	0	0	0	0	0
LEER	0	0	0	0	0	0	0	0	0	0	0	0
CADR	0	0	0	0	0	0	0	0	0	0	0	0
ERMO	0	0	0	0	0	0	0	0	0	0	0	0
Other forbs	13	10	13	25	75	62	8	26	25	19	24	49
TOTAL	446	418	562	684	504	1165	134	325	340	278	249	390

were also similar on each sampling date. Because ordination diagrams, which included all sampling dates, contained too many points to plot adequately, only results from the October 1985 sampling date are shown.

Effects of *J. pinchotii* on herbaceous vegetation pattern were recognizable at several scales (landscape, community, and individual tree). Evaluation of pattern at the landscape level involved ordinating all trees on both sites (Fig. 1). The first ordination axis indicates a site effect: all quadrats from the relict site were assigned negative first axis scores, and most quadrats from the grazed site were

TABLE 1 continued. Data for 1985.

Species[1]	GRAZED SITE											
	July 1985						October 1985					
	Location						Location					
	1	2	3	4	5	I	1	2	3	4	5	I
GRASSES												
ARSP	2	61	393	586	347	570	0	16	64	211	188	228
BOCU	114	198	19	27	49	186	8	79	0	0	0	209
BUDA	0	12	18	13	19	41	17	8	8	7	22	7
TRMU	8	118	50	54	83	127	4	114	34	85	172	181
STNE	0	0	0	0	0	0	0	0	0	0	0	0
SIHY	120	2	0	0	0	0	126	0	0	0	0	0
Other grasses	0	114	38	134	118	80	2	187	82	184	204	13
FORBS												
CRDI	0	109	190	145	230	127	0	50	131	68	118	30
SICA	390	2	0	0	13	0	0	4	0	0	0	0
ZIGR	0	65	0	0	0	94	0	36	119	53	31	48
EVNU	0	13	38	24	71	100	0	24	34	65	33	45
LEER	14	37	132	83	101	82	169	476	436	152	212	20
CADR	8	12	26	43	127	57	0	44	20	7	133	43
ERMO	10	312	79	36	13	46	57	57	90	63	85	67
Other forbs	145	185	292	273	211	474	77	174	150	158	134	184
TOTAL	811	1240	1275	1418	1382	1984	460	1269	1168	1053	1332	1075
	RELICT SITE											
GRASSES												
ARSP	0	107	135	83	183	88	0	16	21	7	113	254
BOCU	0	463	417	351	379	595	91	356	609	615	830	605
BUDA	0	45	35	55	44	26	5	15	8	11	18	45
TRMU	0	47	46	42	33	2	57	274	43	54	60	23
STNE	25	796	247	186	277	25	0	0	0	0	0	10
SIHY	245	117	57	0	0	27	252	66	1	0	0	0
Other grasses	0	74	106	54	64	173	38	280	177	226	82	162
FORBS												
CRDI	0	0	2	0	0	0	0	0	0	0	0	0
SICA	131	145	41	16	0	9	3	39	3	0	0	3
ZIGR	0	0	0	0	0	0	0	0	0	0	0	0
EVNU	0	0	0	0	3	0	0	0	0	0	0	0
LEER	0	0	0	0	0	0	0	0	0	0	0	0
CADR	0	0	0	0	0	0	0	6	2	0	0	0
ERMO	191	123	74	138	84	134	223	180	117	42	111	139
Other forbs	53	91	255	139	349	186	50	52	43	79	69	35
TOTAL	645	2008	1415	1064	1416	1265	719	1284	1024	1034	1283	1276

[1] Species abbreviations are: ARSP = *Aristida* sp., BOCU = *Bouteloua curtipendula*, BUDA = *Buchloe dactyloides*, TRMU = *Tridens muticus*, STNE = *Stipa neomexicana*, SIHY = *Sitanion hystrix*, CRDI = *Croton dioicus*, SICA = *Simsia calva*, ZIGR = *Zinnia grandiflora*, EVNU = *Evolvulus nuttallianus*, CADR = *Calylophus drummondianus*, ERMO = *Erigeron modestus*.

[2] Locations are midway between tree bole and dripline (1), at dripline (2), 1, 2, and 3 m from dripline (3–5, respectively), and in interstices (I).

assigned positive first axis scores. Exceptions were quadrats under tree canopies (location 1 and, to a limited extent, location 2) on the grazed site.

Ordination of quadrats along the second axis (Fig. 1) indicates a gradient from tree bole to interstice representing tree influence on herbaceous vegetation. Location 1 quadrats (under the tree canopy) were ordinated together, as were quadrats beyond the canopy edge (locations 3–5, I). Quadrats at the canopy edge (location 2) were ordinated

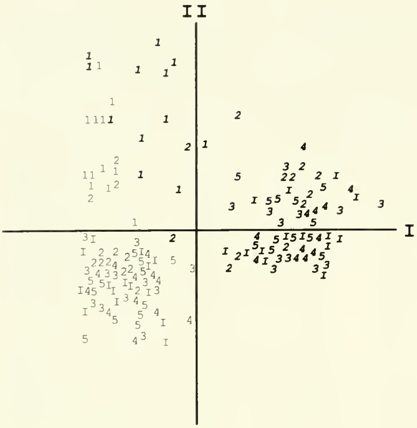


Fig. 1. Reciprocal averaging quadrat ordination around *Juniperus pinchotii* Sudw. trees on grazed (bold type) and relict (normal type) semiarid grasslands. Location 1 is at midpoint between tree bole and canopy edge; location 2 is at canopy edge; and locations 3, 4, and 5 are 1, 2, and 3 m from canopy edge, respectively. Location I is in interstice between trees.

between quadrats under the tree and those beyond the canopy edge.

Ordination of all trees on the relict site (Fig. 2) and the grazed site (Fig. 3) reflects community-level analyses. On both sites, axis I reflected a distance gradient from tree bole to interstice. Quadrats under the canopy and at canopy edge were assigned negative first axis ordination scores, whereas other quadrat locations were generally assigned positive scores. Additionally, quadrats at locations 3–5 were ordinated together with quadrats from the interstitial zone. Axis II reflected tree-to-tree variation. Small trees (height, stem diameter, and crown volume) were ordinated more positively on this axis than were large trees (data not shown). Ordinations did not indicate any effect of compass direction on herb response.

Ordination of a single tree on each site further elucidated the tree's influence on herbaceous vegetation beneath the canopy (Figs. 4, 5; in each case, axis III was plotted against axis I to reduce arch distortion associated with the plot of axes I and II). The ordination revealed that quadrats under the tree (location 1) were readily distinguishable from remaining quadrats. Quadrats 1, 2, and 3 m from the tree (locations 3, 4, and 5) tended to be ordinated together. Quadrats at canopy edge (location 2) were assigned ordination scores intermediate between these two groups.

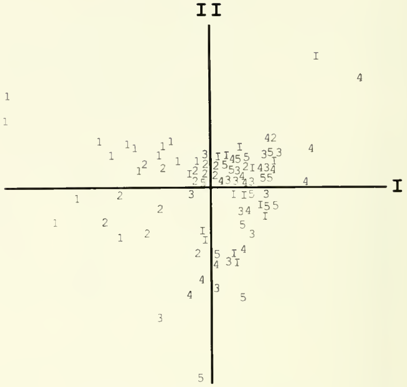


Fig. 2. Reciprocal averaging quadrat ordination around *Juniperus pinchotii* Sudw. trees on a relict semiarid grassland. Location 1 is at midpoint between tree bole and canopy edge; location 2 is at canopy edge; and locations 3, 4, and 5 are 1, 2, and 3 m from canopy edge, respectively. Location I is in interstice between trees.

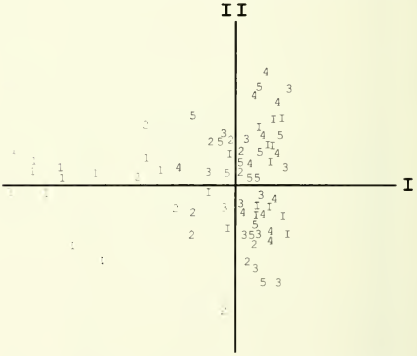


Fig. 3. Reciprocal averaging quadrat ordination around *Juniperus pinchotii* Sudw. trees on a grazed semiarid grassland. Location 1 is at midpoint between tree bole and canopy edge; location 2 is at canopy edge; and locations 3, 4, and 5 are 1, 2, and 3 m from canopy edge, respectively. Location I is in interstice between trees.

Soil Properties

Organic matter, soil P, and pH differed ($P < .05$) between sites; however, trees influenced few of the measured soil properties.

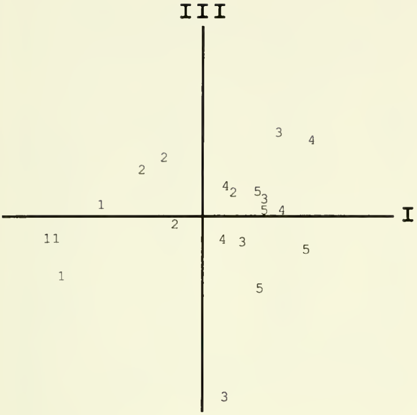


Fig. 4. Reciprocal averaging ordination around a *Juniperus pinchotii* Sudw. tree on a relict semiarid grassland. Location 1 is at midpoint between tree bole and canopy edge; location 2 is at canopy edge; and locations 3, 4, and 5 are 1, 2, and 3 m from canopy edge, respectively.

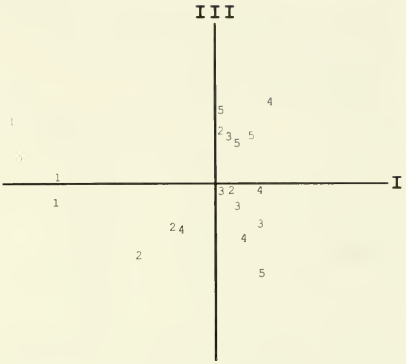


Fig. 5. Reciprocal averaging ordination around a *Juniperus pinchotii* Sudw. tree on a grazed semiarid grassland. Location 1 is at midpoint between tree bole and canopy edge; location 2 is at canopy edge; and locations 3, 4, and 5 are 1, 2, and 3 m from canopy edge, respectively.

Organic matter was higher ($P < .05$) under trees than at or beyond canopy edge on both sites (Table 2). Potassium and salinity were slightly higher at the edge of the canopy than at other locations on the relict site. Other soil properties were unaffected by distance from tree bole.

DISCUSSION

These data indicate that site differences reflecting differences in environment and possibly grazing history had a relatively large impact on soils and herbaceous vegetation. Although parent material and physical environment appeared similar for the two sites, these sites may have differed with respect to localized precipitation patterns or geochemical processes. It is also noteworthy that these two study areas have different histories with respect to livestock grazing. Livestock grazing can influence these soil properties (Whitehead 1970, Kleiner and Harper 1972, Bauer et al. 1987).

Our data indicate that *J. pinchotii* trees had minimal impact on most soil properties, results which differ markedly from those reported for *Juniperus* species in the western U.S. (for a review see Tiedemann 1987). For example, Barth (1980), Thran and Everett (1987), and Klopatek (1987) found 1.5–5.5 times more soil N under pinyon or juniper trees than in interstices. Concentrations of soil P, K, Mg, Ca, and Na followed similar patterns. However, Brotherson and Osayande (1980) reported no differences in P or cations and only a slight difference in N (0.049 vs. 0.044%) under *J. osteosperma* trees and in open areas. Mean soil N was 0.015% in our study area, which is probably growth-limiting. Tiedemann (1987) indicated that 0.05–0.5% total N is sufficient for grassland and shrubland soils. Differences in soil organic matter at different distances from the bole probably resulted from deposition and subsequent decomposition of *Juniperus* foliage.

Herbs in location 1 and, to a lesser extent, location 2, were protected from grazing by *Juniperus* trees. *Juniperus pinchotii* is a closed-canopy species that does not self-prune lower branches. This growth form offers protection from grazing under canopies. At each site, *J. pinchotii* had little influence on herbaceous vegetation or soil properties beyond the tree crown. Our results indicate less tree influence on herbaceous vegetation than commonly reported for *Juniperus* species in the western U.S. That there was no discernible pattern in herbaceous vegetation 1–3 m past the tree canopy and beyond into the interstitial zone does

TABLE 2. Soil properties of grazed and relict grassland at five locations around *Juniperus pinchotii* trees in western Texas.

Soil property	Site[2]	Location[1] 1	2	3	4	5
OM (%)	R	4.2aA[3]	3.4b	3.3bA	3.4bA	3.4bA
	G	3.5aB	2.9b	2.5cB	2.5cB	2.5cB
K (ppm)	R	490.0b	568.0a	437.0b	435.0b	460.0b
	G	461.0	593.0	494.0	451.0	661.0
Salinity (ppm)	R	358.0ab	374.0a	318.0b	325.0b	342.0b
	G	315.0	329.0	297.0	310.0	316.0
P (ppm)	R	6.5A	7.0A	6.2A	7.8A	7.5A
	G	19.9B	17.3B	18.3B	17.7B	17.1B
pH	R	8.0	7.8A	7.9A	7.8	7.9A
	G	8.0	8.2B	8.1B	8.0	8.1B

[1] Locations are midway between tree bole and dripline (1), at dripline (2), and 1, 2, and 3 m from dripline (3, 4, and 5, respectively).

[2] R relict site, G grazed site.

[3] Means within a row followed by the same lowercase letter are not significantly different ($P > .05$) according to Fisher's protected LSD. Means within a column for each soil property followed by the same uppercase letter are not significantly different ($P > .05$) according to Fisher's protected LSD.

not imply that herbaceous vegetation has not reacted to the presence of *J. pinchotii* trees, but rather that this response is distance-independent. That is, it is likely that interaction between *J. pinchotii* and herbaceous vegetation is similar 1 m from the tree canopy and 5 m beyond the tree canopy. Personal observations of mechanically uprooted *J. pinchotii* trees have revealed that the root system of these trees is laterally extensive. Furthermore, soils of our study areas were less than 50 cm deep and were underlain by indurated caliche (McPherson et al. 1988); these conditions are conducive to lateral root growth. Plummer (1958) and Arnold (1964) also reported *Juniperus* roots in openings between trees, and Johnsen (1962) found many juniper roots up to 16 m from trees. Lateral roots in the latter study commonly exceeded tree heights by threefold. Therefore, the concept of "interstitial zone" may have meaning only in an "aboveground" sense in our study area (where average juniper density is 2123 trees/ha on the grazed site and 288 trees/ha on the relict site [McPherson et al. 1988]). At these tree densities, there may be no zone underground where root occupancy between *J. pinchotii* and herbaceous vegetation is minimal. This interpretation is supported by *J. pinchotii* trees in our study area ranging in age from less than 10 yr to 120 yr old (McPherson 1987). Although *J. pinchotii* is increasing in density in the area, it is not a recent invader of the site, and the older, larger trees are well established and are assumed to have extensive lateral root systems.

The presence of tree-×-quadrat location interaction in our study is of considerable interpretational importance. This interaction indicates that the response of most herbs to distance from *J. pinchotii* depends upon particular characteristics of the tree in question, and precludes general statements about herbaceous pattern related to distance from *J. pinchotii* plants. Contrary to most other studies, we found little discernible zonation beyond the tree canopy. We attribute this interaction to the effect of tree size on vegetation *immediately* beneath the tree (our trees ranged from 1 to 4 m tall). This zone increases with increasing tree size, so that the variation in herbaceous vegetation between locations 1 (midway between tree bole and canopy edge) and 2 (at canopy edge) is strongly influenced by tree size (see Schott and Pieper [1985] for a detailed study on the effect of tree size/age characteristics on resulting subcanopy microenvironment and vegetation). The importance of differences in microclimate associated with compass directions (Arnold 1964, Everett et al. 1983, Armentrout and Pieper 1988) apparently was masked by other factors in our study.

Existence of herbaceous zonation patterns beyond the tree canopy depends upon species and age of *Juniperus* involved, composition of surrounding herbaceous vegetation, and environment (Arnold 1964, Everett et al. 1983, Engle et al. 1987, Armentrout and Pieper 1988). In arid and semiarid environments there is often a reduction in intensity of competition with improvement of soil water status (see Fowler [1986] for a review). We suggest that herbaceous zonation beyond the tree canopy is more likely to develop around western junipers in drier environments (e.g., *J. osteosperma* in Everett et al. 1983) than around eastern junipers in more mesic environments (e.g., *J. virginiana* in Engle et al. 1987) because limiting moisture in the former setting intensifies species interactions. Superimposed on this "environmental" effect is the influence of herbaceous species composition (e.g., Armentrout and Pieper 1988). This interpretation is consistent with the observation that *J. pinchotii* is a stabilized hybrid between two western junipers (*J. deppeana* and *J. monosperma*) (Hall 1963, Hall and Carr 1968, Adams 1972, 1975) which, by virtue of its increasing density in western and central Texas grasslands, is evidently well adapted to a moisture regime more favorable than that experienced by its progenitors.

It is noteworthy that effects of *J. pinchotii* on herbaceous vegetation pattern were recognizable at several scales (landscape, community, and individual tree). Arnold (1964) first described herbaceous vegetation patterns around *Juniperus* using a single tree. Subsequent research (e.g., Clary 1973, Springfield 1976, Everett et al. 1983, Schott and Pieper 1985) increased the sample size but still focused on the impact of individual trees on herbaceous vegetation patterns. Our study indicates that patterns detectable at the level of individual trees may also be identified at much larger scales.

ACKNOWLEDGMENTS

We thank Sheila Merrigan, Colleen Schreiber, and Jeff Mosley for their assistance with data collection. Mykal Ryan assisted with data entry. This study is a contribution of the College of Agricultural Sciences, Texas Tech University, Publication Number T-9-570.

LITERATURE CITED

Adams, R. P. 1972. Chemosystematic and numerical studies of natural populations of *Juniperus pinchotii* Sudw. Taxon 21: 407–427.

———. 1975. Numerical-chemosystematic studies of intraspecific variation in *Juniperus pinchotii*. Biochemical Systematics and Ecology 3: 71–74.

Armentrout, S. M., and R. D. Pieper. 1988. Plant distribution surrounding Rocky Mountain pinyon pine and one seed juniper in south-central New Mexico. Journal of Range Management 41: 139–143.

Arnold, J. F. 1964. Zonation of understory vegetation around a juniper tree. Journal of Range Management 17: 41–42.

Barth, R. C. 1980. Influence of pinyon pine trees on soil chemical and physical properties. Soil Science Society of America Journal 44: 112–114.

Bauer, A., C. V. Cole, and A. L. Black. 1987. Soil property comparisons in virgin grasslands between grazed and nongrazed management systems. Soil Science Society of America Journal 51: 176–182.

Brotherson, J. D., and S. T. Osayande. 1980. Mineral concentrations in true mountain mahogany and Utah juniper, and in associated soils. Journal of Range Management 33: 182–185.

Brown, J. W., and J. L. Schuster. 1969. Effects of grazing on a hardland site in the southern High Plains. Journal of Range Management 22: 418–423.

Clary, W. P. 1973. Effects of Utah juniper removal on herbage yields from Springerville soils. Journal of Range Management 24: 373–378.

Correll, D. S., and M. S. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas. 1881 pp.

Dixon, M. L. 1975. Soil survey of Borden County, Texas. USDA Soil Conservation Service, Washington, D.C. 68 pp.

Dixon, M. L., W. H. Dittemore, and H. W. Hyde. 1973. Soil survey of Scurry County, Texas. USDA Soil Conservation Service, Washington, D.C. 56 pp.

Ellis, D., and J. L. Schuster. 1968. Juniper age and distribution on an isolated butte in Garza County, Texas. Southwestern Naturalist 13:343–348.

Engle, D. M., J. F. Stritzke, and P. L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. Journal of Range Management 40: 237–239.

Everett, R. L., S. H. Sharrow, and R. O. Meeuwig. 1983. Pinyon-juniper woodland understory distribution pattern and species associations. Bulletin of the Torrey Botanical Club 110:454–463.

Fireman, M., and H. E. Hayward. 1952. Indicator significance of some shrubs in the Escalante Desert, Utah. Botanical Gazette 114: 143–155.

Follett, R. H. 1969. Zn, Fe, Mn, and Cu in Colorado soils. Unpublished dissertation, Colorado State University, Fort Collins. 138 pp.

Fowler, N. L. 1986. The role of competition in plant communities in arid and semiarid regions. Annual Review of Ecology and Systematics 17: 89–110.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York. 298 pp.

Hall, M. T. 1963. Variation and hybridization in *Juniperus*. Annals of the Missouri Botanical Garden 39:1–64.

Hall, M. T., and C. J. Carr. 1968. Variability in *Juniperus* in the Palo Duro Canyon of west Texas. Southwestern Naturalist 13:75–98.

Hibbard, P. L. 1940. Accumulation of zinc in soils under persistent vegetation. Soil Science 59:53–55.

Johnsen, T. N. 1962. One-seed juniper invasion of northern Arizona grasslands. Ecological Monographs 32: 187–207.

KLEINER, E. F., AND K. T. HARPER. 1972. Environment and community organization in grasslands of Canyonlands National Park. Ecology 53:299–309.

KLOPATEK, J. M. 1987. Nutrient patterns and succession in pinyon-juniper ecosystems of northern Arizona. Pages 391–396 *in* R. L. Everett, compiler, Proceedings—Pinyon-Juniper Conference. USDA Forest Service Intermountain Experiment Station General Technical Report INT-215, Ogden, Utah. 581 pp.

MCLEAN, E. O. 1982. Soil pH and lime requirement. Pages 199–223 *in* A. L. Page, ed., Methods of soil analysis, part II. American Society of Agronomy, Madison, Wisconsin. 1142 pp.

MCPHERSON, G. R. 1987. Plant interactions in redberry juniper–mixed grass communities. Unpublished dissertation, Texas Tech University, Lubbock. 87 pp.

MCPHERSON, G. R., AND H. A. WRIGHT. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. American Midland Naturalist 122:144–151.

MCPHERSON, G. R., H. A. WRIGHT, AND D. B. WESTER. 1988. Patterns of shrub invasion in semiarid Texas grasslands. American Midland Naturalist 120: 391–397.

ONKEN, A. B., R. MATHESON, AND E. J. WILLIAMS. 1980. Evaluation of EDTA-extractable phosphorus as a soil test procedure. Soil Science Society of American Journal 44:783–792.

PLUMMER, A. P. 1958. Restoration of juniper-pinyon ranges in Utah. Pages 207–211 *in* Proceedings—Society of American Foresters 58th Annual Meeting. Society of American Foresters, Washington, D.C. 215 pp.

PRINCE, A. L. 1955. Methods in soil analysis. Pages 328–362 *in* F. E. Bear, ed., Chemistry of the soil. American Chemical Society Monograph 126. 373 pp.

RICHARDS, L. A., ED. 1954. The diagnosis and improvement of saline and alkali soils. USDA Agriculture Handbook No. 60, Washington, D.C. 160 pp.

SCHOTT, M. R., AND R. D. PIEPER. 1985. Influence of canopy characteristics of one-seed juniper on understory grasses. Journal of Range Management 38:328–331.

SHARMA, M. L., AND D. J. TONGWAY. 1973. Plant induced soil salinity patterns in two saltbush (*Atriplex* sp.) communities. Journal of Range Management 26:121–125.

SPRINGFIELD, H. W. 1976. Characteristics and management of southwestern pinyon-juniper ranges: the status of our knowledge. USDA Forest Service Rocky Mountain Experiment Station Research Paper RM-160, Fort Collins, Colorado. 32 pp.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. 2nd ed. McGraw-Hill Book Co., New York. 633 pp.

THRAN, D. F., AND R. L. EVERETT. 1987. Soil nutrient changes following tree harvest. Pages 387–390 *in* R. L. Everett, compiler, Proceedings—Pinyon-Juniper Conference. USDA Forest Service Intermountain Experiment Station General Technical Report INT-215, Ogden, Utah. 581 pp.

TIEDEMANN, A. R. 1987. Nutrient accumulations in pinyon-juniper ecosystems—managing for future site productivity. Pages 352–355 *in* R. L. Everett, compiler, Proceedings—Pinyon-Juniper Conference. USDA Forest Service Intermountain Experiment Station General Technical Report INT-215, Ogden, Utah. 581 pp.

WHITEHEAD, D. C. 1970. The role of nitrogen in grassland productivity. Commonwealth Agriculture Bureau Bulletin 48. Farnham Royal, Bucks, England. 202 pp.

Received 20 March 1991
Accepted 5 August 1991

Great Basin Naturalist 51(4), 1991, pp. 325–335

TWO NEW SPECIES OF *AUREALCAULIS* (OSMUNDACEAE) FROM NORTHWESTERN NEW MEXICO

William D. Tidwell[1] and David A. Medlyn[2]

ABSTRACT.—Two new osmundaceous species, *Aurealcaulis moorei* and *A. bransonii*, are described from the San Juan Basin of northwestern New Mexico. The area from which they were collected is uncertain, but it is presumed they came from the Lower Eocene San Jose Formation near Angel Peak, southeast of Bloomfield, New Mexico. The species are characterized by having a heterogeneous (*A. moorei*) to homogeneous (*A. bransonii*) pith, non- or partial closure of their leaf gaps, exarch protoxylem clusters, formation of their C-shaped leaf traces by fusion of two segments from adjacent xylem strands in their inner cortices, relatively low numbers of traces in their cortices (16–22 in *A. moorei*, 15–19 in *A. bransonii*), roots arising from lateral margins of these segments, sclerenchymatous outer cortex that connects with the sclerotic ring of the petiolar vascular strand, crenate (*A. moorei*) or interrupted (*A. bransonii*) sclerenchyma lining the adaxial concavity of their petiole strands, and leaf bases that may or may not contain one, occasionally two, sclerotic cellular masses in their stipular wings in *A. moorei* and 6–8 more or less aligned masses in *A. bransonii*. They are compared with other osmundaceous taxa, particularly *A. crossii* Tidwell & Parker of Paleocene age. Because of variations in these new species, *Aurealcaulis* Tidwell & Parker is slightly emended to accept species of this genus with heterogeneous or homogeneous piths, protoxylem becoming endarch in the leaf traces, petiolar vascular strands formed by fusion of segments from the xylem strands in the inner cortex, outer cortex, or outside the stem, and the occurrence or nonoccurrence of sclerenchyma in the adaxial concavity of their petiolar vascular stands and in their stipular wings. The paleoecological conditions under which these species of *Aurealcaulis* grew are also considered.

Key words: Aurealcaulis, *Osmundaceae, New Mexico, Eocene, San Juan Basin, San Jose Formation.*

Aurealcaulis Tidwell & Parker (1987) has a rather limited fossil record at present, but with the addition of the two new species described in this report from the San Juan Basin, New Mexico, and a third as yet unreported one from near the Black Hills, South Dakota, it seems to have been an important, albeit small, component of Early Tertiary floras. The genus also appears to have possibly occurred higher in the Tertiary before it became extinct and was more widely distributed than previously known.

The definite age and collection site for the specimens upon which this paper is based are currently unknown. Portions of them were donated first by Mr. Doug Moore of Glendora, California, who assumed they were collected from the Upper Jurassic Morrison Formation in Lisbon Valley of east central Utah (Tidwell et al. 1989). Mr. William Branson of Helper, Utah, from whom Mr. Moore had originally obtained the specimens, corrected this information and stated he had in turn acquired them from Mr. J. B. Sanchez of San Juan Gems of Cortez, Colorado. An unknown collector had sold them to Mr. Sanchez, and the only information he had was that they were collected near Farmington, New Mexico, and had been purchased with fossil wood preserved as bright yellow jasper. The fossil wood was traced to the Upper Cretaceous Kirtland Shale northwest of Farmington, but the ferns were never found. The ferns, however, are anatomically more advanced than *Aurealcaulis crossii* of Paleocene age and therefore are most likely from the Lower Eocene San Jose Formation, presumably from an area east of Angel Peak, southeast of Bloomfield, New Mexico. Considerable time and money have been spent attempting to locate the site, but the effort as yet has been unsuccessful.

Reports of fossil plants in the stratigraphic units from the Angel Peak region are rather sparse. Numerous fossil vertebrates, however, have been described from the Paleocene

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.
[2] Life Span Learning Class Division, Utah State University, Logan, Utah 84321.

Nacimiento Formation on the west side of the peak (Wilson 1951, Taylor 1981). Although abundant undescribed fossil woods occur in the San Jose Formation, the only fossil plants previously recorded from the formation in this general area are compressional-impressional material from nearby Santos Peak (Tidwell et al. 1981). This small flora of leaves and leafy shoots consists of 15 species representing ferns, conifers, and flowering plants. The ferns include fragments of the leaves of *Acrostichum hesperium* and specimens of probable *Danaea*.

This report of *Aurealcaulis* species from New Mexico is significant because they are the first permineralized specimens of Osmundaceae and only the second report of osmundaceous fossils from this state. Leaves assignable to *Cladophlebis* sp. and *Osmunda hollicki* Knowlton were previously reported from the Upper Cretaceous Fruitland-Kirkland Formations in the San Juan Basin (Tidwell et al. 1981). Knowlton (1917) described *O. hollicki* from the Upper Cretaceous Vermejo Formation across the border near Wallsburg, Colorado, and the senior author collected osmundaceous leaves, but did not report them, from a coal mine in the Paleocene Raton Formation west of Raton, New Mexico.

TAXONOMY

Aurealcaulis Tidwell & Parker, emended

EMENDED DIAGNOSIS.—Fossil osmundaceous rhizomes, arborescent or erect axes, surrounded by a mantel of leaf bases and adventitious roots; dissected ectophloic siphonostele or ectophloic dictyostele; xylem cylinder 10 or more tracheids thick, high number xylem strands, leaf gaps delayed, high, and wide; pith homogeneous or heterogeneous; cortex differentiated into inner and outer tissues; leaf traces often found in two segments, adaxially curved, protoxylem exarch, fusing and becoming endarch in inner cortex, outer cortex, or outside stem; petioles stipulate; sclerenchyma lining petiolar vascular strands may or may not be present; sclerotic ring homogeneous; stipular wings with or without sclerenchyma; roots diverge from leaf traces in inner cortex.

Aurealcaulis moorei, sp. nov.

Figs. 1A-B, 2, 3A

DIAGNOSIS.—Erect or arborescent, stem 14–16 mm in diameter, surrounded by leaf bases and roots; stele 7–8 mm across, dissected ectophloic siphonostele; pith 2–2.5 mm across, heterogeneous; xylem cylinder dissected, 32–36 xylem strands separated by leaf gaps, strands 15–18 tracheids thick radially, gaps lack closure, protoxylem exarch; phloem external; inner cortex 0.7–1 mm wide, parenchymatous; outer cortex homogeneous, 2–3 mm wide, sclerenchymatous; 16–22 leaf traces per transverse section of cortex; departing leaf trace two segments originating from adjacent xylem strands, fused into C-shaped trace in inner cortex; protoxylem becoming endarch, petiolar vascular strand curved, sclerotic tissue adaxially flattened, becoming crenate; sclerotic ring homogeneous, sclerenchymatous; stipular wings may or may not contain one, occasionally two, large, round cellular masses of sclerenchyma in each wing; roots arise from lateral edge of segments of traces in inner cortex.

REPOSITORY.—Brigham Young University 5041 (HOLOTYPE).

LOCALITY.—Uncertain, possibly the eastern slope of Angel Peak, northwestern New Mexico.

HORIZON.—Uncertain, possibly the San Jose Formation.

AGE.—Uncertain, possibly Early Eocene.

ETYMOLOGY.—The specific epithet is for Mr. Doug Moore of Glendora, California, for donating the specimens for this study.

DESCRIPTION.—The specimen (90 mm across × 85 mm tall) of *A. moorei* consists of a stem surrounded by petiole bases and adventitious roots (Figs. 1A, 2A, 3A). The base of the specimen is composed of roots and distorted leaf bases. A column of parenchyma cells 78–97 μm in diameter in the center and a zone of thick-walled sclerotic tissue 6–10 cells wide around its periphery form the heterogeneous pith (Fig. 2F). The diameters of the sclerenchyma cells vary between 85 and 120 μm with walls 10 μm thick. The sclerenchyma typically projects into the leaf gaps for a short distance. Most of the parenchyma cells in the center of the pith have been destroyed and replaced with mineral matter.

The xylem cylinder is 2–3 mm across and contains 32–36 strands of xylem separated by

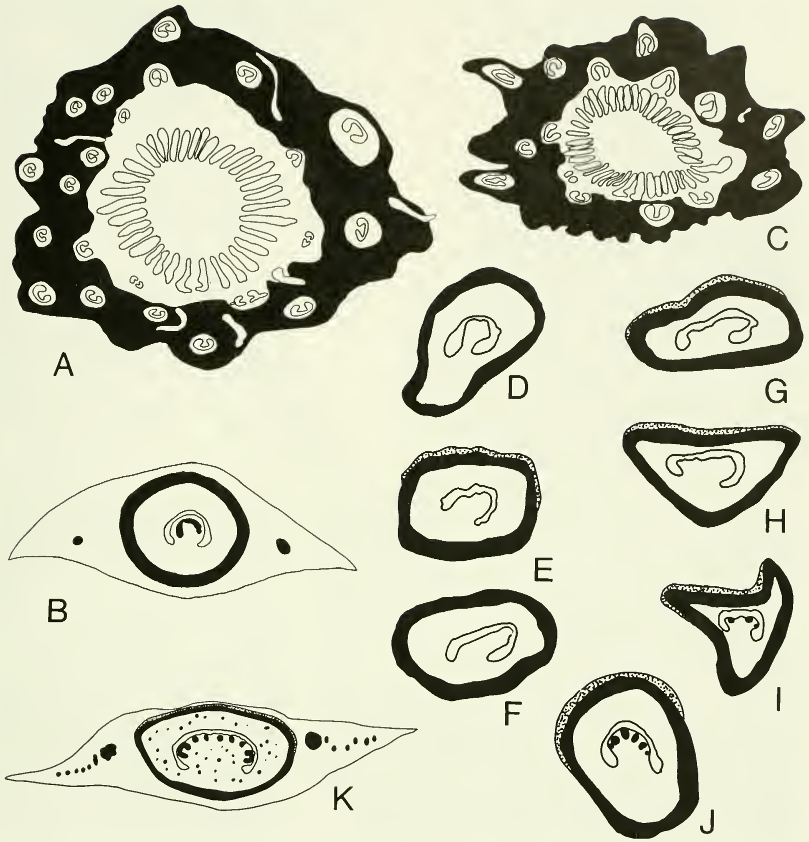
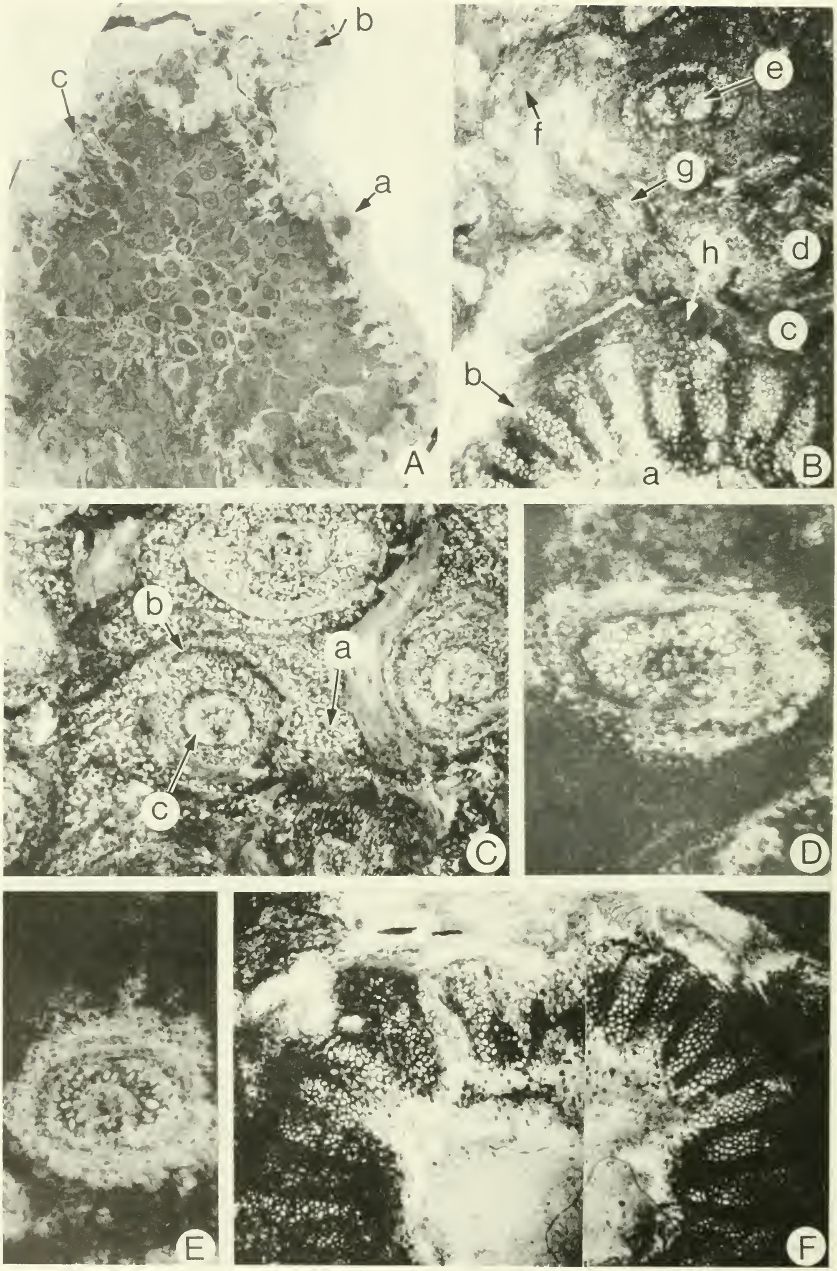


Fig. 1. A–B. *Aurealcaulis moorei* sp. nov. (5041, 1): A, stem, X4; B, petiole with attached stipular wings; note masses of sclerenchyma in each wing, X5; C–K, *Aurealcaulis bransonii* sp. nov. (5042, 1); C, stem X4; D–J, sequence of petioles from stem outward; note heterogeneous sclerotic rings in E, G–J, X5; K, petiole with attached stipular wings illustrating the abundance of sclerenchyma in the petioles and wings, X5. Black = sclerenchyma and sclerotic outer cortex of the stems (all transverse sections).

complete leaf gaps that do not show closure (Figs. 2B, 2F). Thus, the strands are distinct and do not connect with one another at any point. They have a radial thickness of 15–18 tracheids and are 3–6 metaxylem tracheids wide. The latter are 40–120 μm wide by 400–650 μm long and have scalariform pitting in their walls. Protoxylem groups are exarch on the external part of each xylem strand with individual elements that are 19–40 μm in diameter.

A poorly preserved, discontinuous zone of thin-walled cells (1–2 cells wide) between the xylem and phloem represents the xylem sheath. It connects with the parenchyma in the leaf gaps. Cells of the gaps are radially elongated, paralleling the margins of the gap, and are 50–60 μm long and 19–38 μm wide. Sclerotic cells similar to those of the outer pith occur about one-third the length of the gap near the pith, and the radially elongated parenchyma cells occupy the remainder.


b
c
a
A
e
f
g
h
d
c
b
a
B
b
a
c
C
D
E
F

Leaf trace development begins when the exarch protoxylem groups on separate, but adjacent, strands face one another and then split off with connecting metaxylem elements, forming two distinct segments (Fig. 2D). These segments fuse and form a single C-shaped trace in the inner cortex (Fig. 2E). The protoxylem groups, one from each segment, become endarch in the trace, eventually dividing into as many as seven protoxylem points in the petiolar vascular strands (Fig. 1B).

Generally, poorly preserved phloem is crushed. The metaphloem appears to be 2–3 cells wide, the cells varying from 19 to 38 μm in diameter. Protophloem is indiscernible.

The endodermis is represented by a line of crushed cells 20 μm wide, filled with dark contents. It is continuous and separates the cortex from the stele.

Parenchymatous tissue of the inner cortex is composed of isodiametric (5–7 μm) cells near the endodermis and appears as a zone of tangentially elongated cells (30–50 μm × 100–150 μm) perpendicular to the xylem strands and surrounding the stele. Leaf traces in the inner cortex are surrounded by parenchymatous cortical cells and a thin endodermis as they leave this tissue. Also, prior to the segments fusing and then leaving this tissue, adventitious roots depart from their outer margins, usually from one segment first and then from the opposite one.

Homogeneous, sclerenchymatous tissue (cells 30–60 μm × 180–400 μm) composing the outer cortex encloses the departing C-shaped leaf traces after the segments have fused. This tissue forms the sclerotic ring around the traces.

At the point of departure, the leaf traces are 1–2 tracheids thick at their centers and 3–4 thick on their flanks (Fig. 2E). Continuous sclerenchyma is present in the adaxial concavities of the traces.

A crushed xylem sheath and phloem, 1–2 cells wide, are abaxial on the xylem of the petiolar vascular strands. A 3-cell-layered endodermis surrounds them, and crenate sclerenchyma is present in the adaxial concavity of these strands. The inner cortex of the petiole is composed of parenchyma cells 30–60 μm in diameter. The fibers of the sclerotic ring are uniform in size, 30–60 μm across, and continuous with those of the outer cortex.

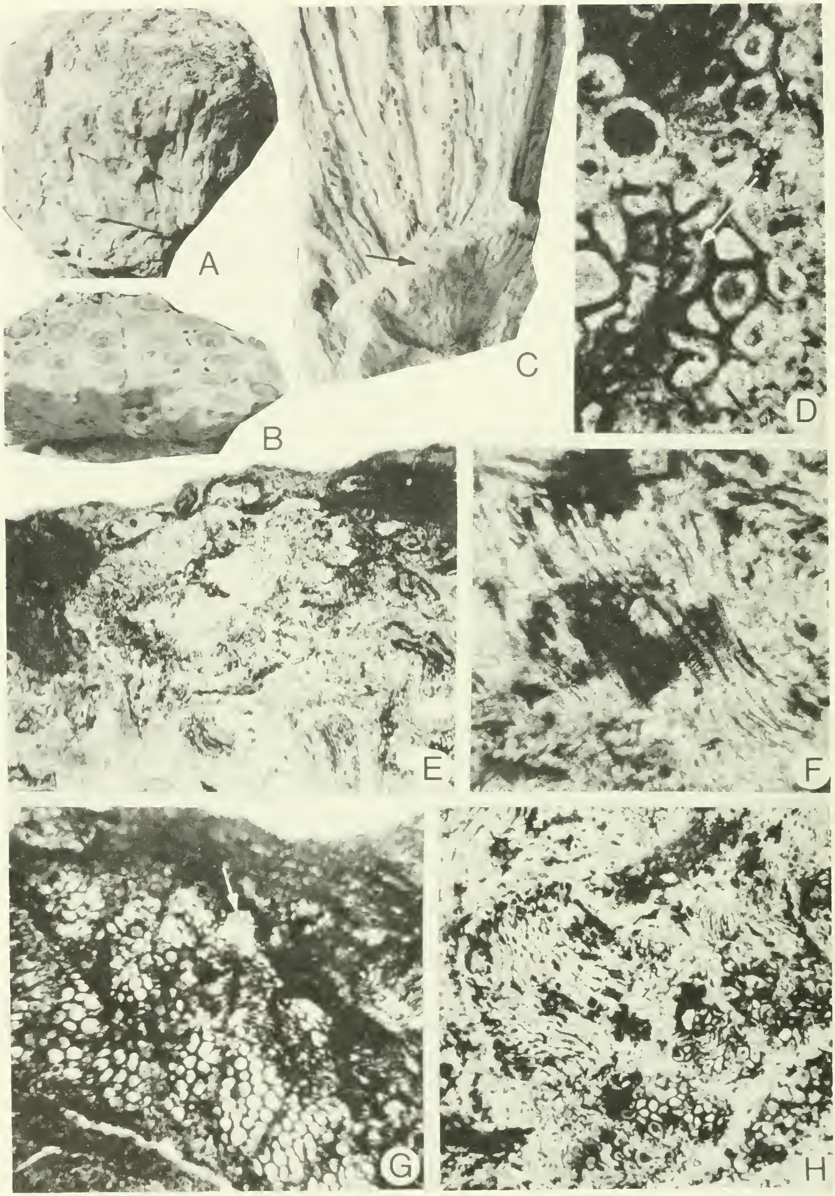
Stipular wings of the leaf bases are shorter at lower levels, becoming longer at higher levels, and are often distorted by penetrating roots. Wing expansions are from 4 to 17 mm from tip to tip, with the parenchyma cells of the wings being 40–80 μm in width and generally filled with dark contents (Fig. 2C). Epidermal cells are 10 μm wide × 30–40 μm in tangential length, and cuticle is not preserved. A 3-cell-wide palisade layer having cells 50–100 μm long × 40 μm wide is present immediately below the abaxial epidermis. One, occasionally two, strands of fibers 40 μm or more across, composed of upwards of 80 cells with each cell being about 10 μm wide, occur approximately one-half the distance between the sclerotic ring and the wing tip (Fig. 1B). Some stipular wings lack these groups of sclerenchyma.

Numerous adventitious roots occur throughout the specimen. They are diarch with the phloem, pericycle and endodermis being crushed. The metaxylem tracheids are 50 μm and the exarch protoxylem tracheal elements 15 μm in diameter. Cells of the parenchymatous inner cortex are 20 μm wide and surrounded by a homogeneous, sclerenchymatous outer cortex. Most of the roots are cut transversely, which suggests an arborescent growth habit (Miller 1971).

COMPARISON.—*Aurealcaulis moorei* is proposed as a new species with the following characteristics: an erect to arborescent habit, a heterogeneous pith, nonclosure of its leaf gaps, formation of its C-shaped trace by fusion in its inner cortex of two segments from adjacent xylem strands, 16–22 traces in its cortices, sclerenchymatous outer cortex that connects with the sclerotic ring of the petiolar

---

Fig. 2 (see facing page). *Aurealcaulis moorei* sp. nov. (all transverse views): A, actual specimen (5041); stem (a) near edge of specimen with petiole bases (b) and roots (c) making up remainder of specimen, X1; B, close-up of a portion of the stem; pith (a), xylem strands (b), inner cortex (c), outer cortex (d), leaf trace (e), oblique section of two segments of a leaf trace, (f) is left side and (g) is right side, which is still attached to xylem strand (h) (5041, 1), X5; C, petiole vascular strands with stipular wings (a) attached; note sclerotic ring (b) surrounding the C-shaped strand (c) (5041, 1), X5; D, two segments of a leaf trace that have not completely fused (5041, 1), X15; E, leaf trace after segments have fused (5041, 1), X10; F, close-up of the xylem strands and the pith (5041, 1), X5.


A
B
C
D
E
F
G
H

vascular strand, leaf bases with crenate-shaped sclerenchyma lining the concavity of their vascular strands, and may or may not contain one, occasionally two, cellular masses of sclerenchyma in their stipular wings.

Aurealcaulis moorei differs from the other species of *Millerocaulis* and *Osmundacaulis* and from living members of the Osmundaceae (Hewitson 1962) in its manner of trace and root origination, its lack of gap closure, and the exarch protoxylem clusters in its xylem strands.

Aurealcaulis moorei can be distinguished from the generitype *A. crossii,* which was reported from the Paleocene Fort Union Formation near Rock Springs, Wyoming (Tidwell and Parker 1987), by its having a heterogeneous pith, fibrous outer cortex, and sclerenchyma in its petiolar strands and stipular wings, all of which are not present in *A. crossii.*

Aurealcaulis bransonii, sp. nov.

Figs. 1C-K, 3B-H, 4

DIAGNOSIS.—Erect, stem 15–20 mm across, surrounded by leaf bases and roots; stele 7 mm × 10 mm in diameter, dissected ectophloic siphonostele; pith 3 mm × 6 mm across, homogeneous, parenchymatous; xylem cylinder dissected, 35–40 xylem strands separated by narrow leaf gaps, strands 17–20 tracheids thick radially and 3–6 metaxylem tracheids wide, gaps generally lack closure, protoxylem exarch; phloem external; inner cortex parenchymatous, narrow, .05 mm wide; outer cortex 10 mm thick, homogeneous, sclerenchymatous; 15–19 leaf traces per cross section of cortices; two segments originating from adjacent xylem strands depart and fuse into C-shaped leaf trace in inner cortex; protoxylem becoming endarch; petiolar vascular strand curved; interrupted sclerenchyma adaxial to strand; sclerotic ring heterogeneous; stipular wings contain 6–8 masses of sclerenchyma aligned from near sclerotic ring to near tip; roots arise from lateral edges of segments of traces before they fuse.

REPOSITORY.—Brigham Young University 5042 (HOLOTYPE); 5043, 5044 (PARATYPES).

LOCALITY.—Uncertain, possibly the eastern slope of Angel Peak, northwestern New Mexico.

HORIZON.—Uncertain, possibly the San Jose Formation.

AGE.—Uncertain, possibly Early Eocene.

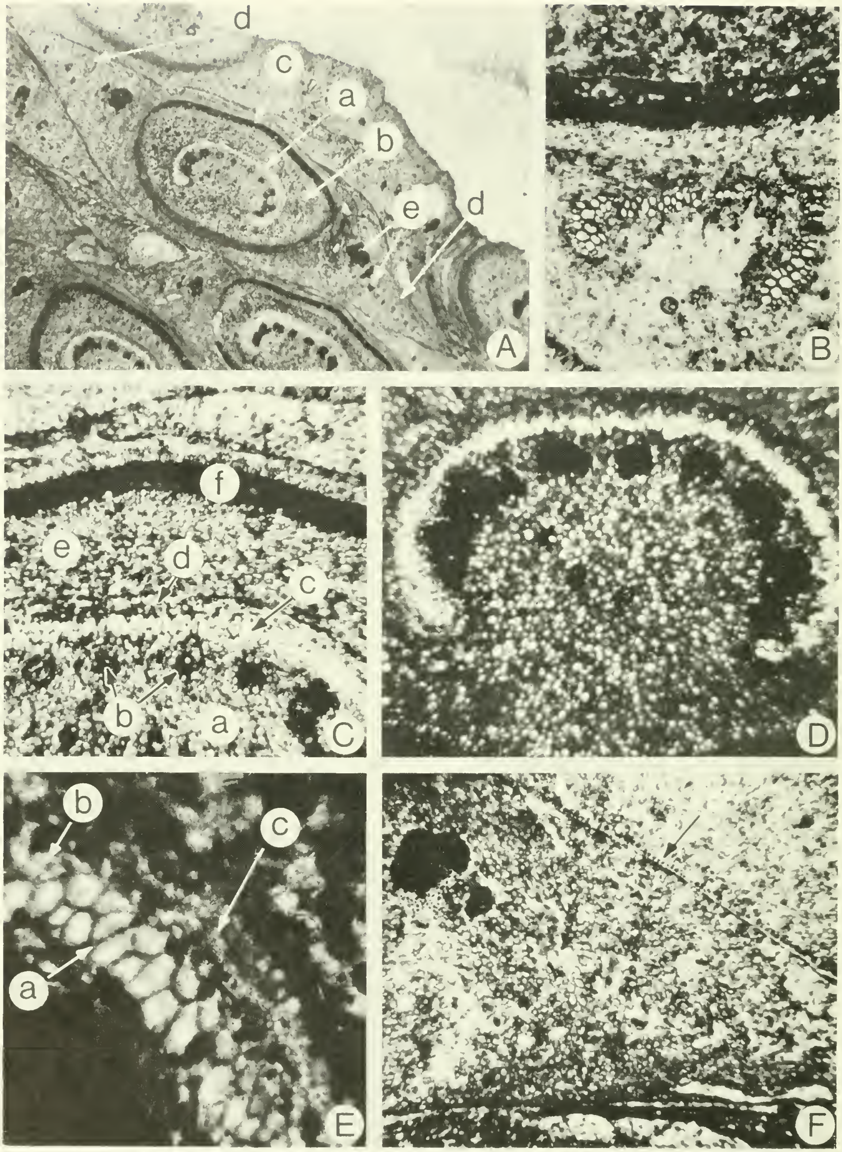
ETYMOLOGY.—The specific epithet is for Mr. William Branson of Helper, Utah, for his assistance with this study.

DESCRIPTION.—The holotype is 100 mm tall × 60 mm across, tapered, flattened, and split in half due to weathering (Fig. 3B). Its stem is present for about one-third the vertical distance of the specimen before it disappears because of erosion, and the leaf traces and petiole bases can be observed at various levels of the petioles (Fig. 3C). Roots appear between the petioles in longitudinal sections; whether they continued outwardly into or bent downwardly into the soil cannot be determined. Paratype (BYU 5043) is fairly large, 150 mm × 250 mm, and without a stem. The specimen is composed primarily of petiole bases, as is the other paratype (BYU 5044). The latter specimen is smaller (25 mm × 75 mm), but its curvature suggests the original was at least 600 mm in diameter.

The isodiametric parenchyma cells of the pith are 70–150 μm in diameter and thin walled. They are filled with dark contents and in some areas are crushed.

The xylem cylinder is 1.5–1.75 mm wide and consists of strands generally separated from one another by the leaf gaps (Figs. 3E, 3G). These strands are only occasionally connected and then by 2–3 tracheids at most. Metaxylem elements in the strands are 70–150 μm wide by 270–900 μm long with scalariform pitting in their multifaceted walls (Fig. 3F). Many of these tracheids are filled with crystals. Their walls vary in thickness from relatively thin (10 μm) to thick (25 μm) with wide (50–120 μm) to narrow (30–70 μm) lumens. Protoxylem elements are also thick walled (Fig. 3D).

Fig. 3 (see facing page). A, Side view of holotype of *Aurealcaulis moorei* sp. nov. (5041), X4; B–H, *Aurealcaulis bransonii* sp. nov. (5042): B, side view of holotype; remains of stem near base (arrow) and roots projecting between petioles, X.75; C, top view of holotype showing transverse sections of petioles; note the stipular wings, X.75; D, close-up of tip of xylem strand illustrating protoxylem cluster (arrow) (5042, 1), X200; E, transverse section of the stem (5042, 1), X7; F, close-up of a longitudinal view of one-half of trace departing xylem strand; note the scalariform thickenings on the tracheid walls (5042, 1), X40; G, close-up of xylem strands; arrow indicates protoxylem cluster (5042, 1), X40; H, close-up of departing trace in longitudinal view (5042, 1), X25.


d
c
a
b
e
d
A
B
f
e
d
c
b
a
C
D
b
c
a
E
F

The phloem is 2–3 cells across and, along with the xylem sheath, pericycle, endodermis, and inner cortex, is poorly preserved. The space originally occupied by the xylem sheath is 20–40 μm wide. It appears to have enclosed the xylem strands and formed the cellular tissue of the gaps.

Formation of the leaf traces and petiole bases is essentially the same as for *A. moorei* (Figs. 3H). The small number of leaf traces (15–19) in transverse section of the cortices and the general nonclosure of the leaf gaps suggest long internodes in this species.

The sclerenchyma in the concavity of the petiolar vascular strand appears at a higher level of the petiole. Initially, it is continuous but eventually becomes interrupted (Figs. 4C, 4D). Two clusters of sclerenchyma fuse together near the tips of the strand, but the remainder remain separate. The fibers of this tissue are angular, thick walled, and 5–12 μm in diameter.

Metaxylem tracheids of the petiolar vascular strands are 30–70 μm across and surrounded by a xylem sheath 1–2 cells wide (Fig. 4E). The phloem is 2–3 cells wide and enclosed by a single-layered pericycle with cells 7–15 μm in diameter and a discontinuous, uniseriate endodermis having cells filled with dark contents. Cells of the inner cortex of the petiole are 20 μm wide and thin walled, with clusters of sclerenchyma occurring irregularly in this tissue (Fig. 4C). Sclerotic rings of the petioles are heterogeneous, with the majority of the cells being thick walled and 30 μm across, whereas the outer, abaxial 12 layers of cells are thinner walled and weather differently from the other cells of the ring. These rows of cells taper to one row on each side of the ring.

The thin-walled parenchyma cells of the stipular wings are 25–30 μm across, and most are filled with contents (Fig. 4F). Cuticle and epidermis of the wings are poorly preserved, with the epidermal cells being 2.5 μm wide. Six to eight masses of sclerenchyma occur in each wing. These masses are aligned from near the sclerotic wing to the tip. The largest near the ring is 300 μm in diameter, whereas the smallest is 150 μm and near the tip. These masses comprise thick-walled fibrous cells 12–15 μm wide.

The roots of *A. bransonii* are like *A. moorei* and weave their courses between the stipular wings of the petioles. Roots invading the wings are relatively rare.

COMPARISON.—*Aurealcaulis bransonii* has a homogeneous pith and partial closure of its leaf gaps similar to *A. crossii*, but unlike *A. moorei*. *Aurealcaulis bransonii* has a lower trace number in its cortices than the other two, interrupted sclerenchyma in the concavity of its petiolar strand, a heterogeneous sclerotic ring, and 6–8 masses of sclerenchyma in its stipular wings, none of which are present in either *A. crossii* or *A. moorei*.

DISCUSSION

Because *A. moorei* and *A. bransonii* vary from the genus *Aurealcaulis* as previously defined (Tidwell and Parker 1987), the genus is emended slightly in this report to contain species assignable to this genus, but having such variations as heterogeneous or homogeneous piths, protoxylem becoming endarch in the leaf traces, petiolar vascular strands formed by fusion of segments from the xylem strands in the inner cortex, outer cortex, or outside of the stem, and occurrence or nonoccurrence of sclerenchyma in the adaxial concavity of their petiolar vascular strands and in their stipular wings.

The occurrence in *Aurealcaulis* of thin-walled cells in its inner cortex, closely adhering petiole bases, and external phloem and endodermis represents a primitive condition for this genus in the Osmundaceae (Miller 1971). The fact that species of *Aurealcaulis* are exarch and arborescent places them among the more primitive members of the family. Based upon seven primitive to advanced characters proposed by Miller (1971) for this family with an additional one specific to

---

Fig. 4 (see facing page). *Aurealcaulis bransonii* sp. nov. (all transverse sections): A, leaf base illustrating petiolar vascular strand (a), outer cortex (b), sclerotic ring (c), and stipular wings (d) containing masses of sclerenchyma (e) (5042, 1), X7; B, close-up of petiolar vascular strand after departing from stem (5042, 1), X25; C, close-up of vascularization of a petiole showing inner cortex (a), sclerenchyma in adaxial configuration of strand (b), xylem (c), phloem (d), outer cortex (e), and sclerotic ring (f) (5042, 1), X25; D, same as Fig. 4C showing more inner cortex of petiole, X25; E, enlargement of a portion of Fig. 4C xylem (a), xylem sheath (b), and phloem (c); endodermis and pericycle are poorly preserved, X75; F, stipular wing containing masses of sclerenchyma; note the epidermis (arrow) (5042, 1), X25.

TABLE 1. Comparison of *Aurealcaulis* species.

	A. crossii Tidwell & Parker	*A. moorei* sp. nov.	*A. bransonii* sp. nov.
Pith	homogeneous	heterogeneous	homogeneous
Xylem strands	55	32–36	35–40
Number of traces in cortex	28–30	16–22	15–19
Outer cortex	not fibrous	fibrous	fibrous
Sclerenchyma in stipular wings	none	may or may not be present	6–8 aligned masses
Age	Paleocene	Lower Eocene(?)	Lower Eocene(?)

Aurealcaulis, *A. bransonii* seems to be the more advanced of these species of *Aurealcaulis* and *A. crossii* the most primitive (Table 1). The general trend of less sclerenchyma in less specialized ferns (Wagner 1964) appears to apply to *Aurealcaulis*. *Aurealcaulis moorei* would be more advanced with its heterogeneous pith, but this is offset by having only an occasional mass of sclerenchyma in its stipular wings and, like *A. crossii*, a homogeneous sclerotic ring. *Aurealcaulis crossii* lacks any sclerenchyma in its wings, a primitive character, whereas *A. bransonii* has 6–8 masses in each wing and is thus more advanced. The inner cortex of the petiole of *A. bransonii* has irregularly shaped clusters of sclerenchyma and a heterogeneous sclerotic ring, both of which are considered advanced characters. These features are lacking in the other two species. Supported by their possible geologic ages, the fusion of the segments in the outer cortex of the older *A. crossii* (Paleocene) may be more primitive than fusion of these segments in the inner cortex of the younger *A. moorei* and *A. bransonii* (possible Eocene). Another probable character is the reduction in the number of strands in the xylem cylinder from 50–60 for *A. crossii* to 32–36 for *A. moorei* and 35–40 for *A. bransonii*.

Among living members of the Osmundaceae, the petioles of *A. bransonii* most closely resemble species of the subgenus *Plenasium*, particularly *Osmunda banksiaefolia* (Hewitson 1962). Distribution of the sclerotic masses in the inner cortices of their petioles and stipular wings is quite similar. The crenate-shaped sclerenchyma lining the adaxial concavity of the strand in *O. banksiaefolia* is like that of *A. moorei* and unlike that of *A. bransonii*, which is interrupted. The xylem cylinders of taxa of the *Plenasium*-type are distinctively different from those of the *Aurealcaulis* species.

The phylogenetic sequence in *Aurealcaulis* is unclear and appears to represent a unique osmundaceous line that became extinct. The ancestor of this genus is unknown. With some modifications, however, earlier members of the *Aurealcaulis* evolutionary line may have arisen from an ancestor common to both them and the subgenus *Plenasium*. It is interesting that a large number of the species of *Millerocaulis* (Tidwell 1986) and most members of *Osmundacaulis* (sensu stricto) appear to be related in some way to the subgenus *Plenasium*. Certainly not all members of *Millerocaulis* and *Osmundacaulis* similar to the *Plenasium* subgenus can be its ancestor (Tidwell 1987). However, if the hypothesis of *Aurealcaulis* and *Plenasium* having a common ancestor is correct, then older forms of *Aurealcaulis* should be encountered eventually.

If these species come from the San Jose Formation, then the environment of the Angel Peak area where *A. moorei* and *A. bransonii* may have occurred can be determined by the associated impression-compression flora (Tidwell et al. 1981), as well as these osmundaceous species. Modern relatives of the flora from Santos Peak occur in moist environments, and living members of the Osmundaceae grow in tropical to cool temperate climates and can be found in bogs, swamps, rain forests, and damp woodlands (Gould 1981). An axis of *A. crossii* was collected in growth position in a lignitic bed of the Fort Union Formation, indicating that this species had grown in swamps. Furthermore, the area in which *A. crossii* occurred seems to have been a forest that grew under swampy conditions on a flat flood plain in a subtropical to warm temperate climate (Brown 1962, Roehler 1979). *Aurealcaulis moorei* and *A. bransonii* very likely grew under similar conditions. It can be concluded, therefore, that the San Juan Basin was, in general, a humid, forested region during the time these plants grew.

ACKNOWLEDGMENTS

The authors thank Mr. Doug Moore for donating the specimens and Mr. William Branson, Mr. Walt Wright of Brea, California, and Drannan Tidwell for aid in attempting to determine the locality.

LITERATURE CITED

BROWN, R. 1962. Paleocene flora of the Rocky Mountains and Great Plains. U.S. Geological Survey Professional Paper 375: 1–119.

GOULD, R. E. 1981. The coal forming flora of the Walloon Coal Measures. Coal Geology (Australia) 1: 83–105.

HEWITSON, W. 1962. Comparative morphology of the Osmundaceae. Annals of the Missouri Botanical Garden 48: 51–93.

KNOWLTON, F. H. 1917. Fossil floras of the Vermego and Raton Formations of Colorado and New Mexico. U.S. Geological Survey Professional Paper 101: 233–435.

MILLER, C. N., JR. 1971. Evolution of the fern family Osmundaceae based on anatomical studies. Contribution of the Museum of Paleontology, University of Michigan 23(8): 105–161.

ROEHLER, H. W. 1979. Geological and energy resources of the Sand Butte Rim NW Quadrangle, Sweetwater County, Wyoming. U.S. Geological Survey Professional Paper 1065-A: A1–A54.

TAYLOR, L. H. 1981. The Kutz Canyon local fauna, Torrejonian (Middle Paleocene) of the San Juan Basin, New Mexico. Pages 242–263 *in* S. Lucas, K. Rigby, and B. Kues, eds., Advances in San Juan paleontology. University of New Mexico Press, Albuquerque.

TIDWELL, W. D. 1986. *Millerocaulis*, a new genus with species formerly in *Osmundacaulis* Miller (fossils, Osmundaceae). Sida 11: 401–405.

_____. 1987. A new species of *Osmundacaulis* (*O. jonesii* sp. nov.) from Tasmania, Australia, Review of Palaeobotany and Palynology 52: 205–216.

TIDWELL, W. D., S. R. ASH, AND L. R. PARKER. 1981. Cretaceous and Tertiary floras of the San Juan Basin. Pages 307–332 *in* S. Lucas, K. Rigby, and B. Kues, eds., Advances in San Juan Basin paleontology. University of New Mexico Press, Albuquerque.

TIDWELL, W. D., D. A. MEDLYN, AND L. R. HARTMAN. 1989. A new osmundaceous taxon from the Morrison Formation (Jurassic) of southeastern Utah. American Journal of Botany Abstracts 76(6): 175.

TIDWELL, W. D., AND L. R. PARKER. 1987. *Aurealcaulis crosii* gen. et sp. nov., an arborescent osmundaceous trunk from the Fort Union Formation (Paleocene), Wyoming. American Journal of Botany 74: 803–812.

WAGNER, W. H., JR. 1964. The evolutionary patterns of living ferns. Memoir of the Torrey Botanical Club 21(5): 86–95.

WILSON, R. W. 1951. Preliminary survey of a Paleocene faunule from the Angel Peak area, New Mexico. University of Kansas Museum of Natural History Publication 5: 1–11.

Received 12 August 1991
Revised 6 September 1991
Accepted 16 September 1991

Great Basin Naturalist 51(4), 1991, pp. 336–342

HOLOCENE BISON FROM ARCHES NATIONAL PARK, SOUTHEASTERN UTAH

Jim I. Mead[1, 2], Saxon E. Sharpe[1], and Larry D. Agenbroad[1,2]

ABSTRACT.—An artifact constructed from a bison (*Bison bison*) hornsheath was recovered from the surface of a sandstone shelter also containing skeletal remains of bison and bighorn (*Ovis canadensis*). Radiocarbon dating of bison, bighorn, and the artifact indicate that all co-occurred on the central Colorado Plateau, southeastern Utah, either between A.D. 1405 and A.D. 1420, or between A.D. 1535 and A.D. 1605. Skeletal remains of the bison imply that the animal was of the local faunal community during the transition between Protohistoric and Historic time.

Key words: bison, Bison, *Holocene, bighorn,* Ovis canadensis, *Colorado Plateau.*

BISON ALCOVE

Bison Alcove (our informal designation for locality 42GR538) is a large shelter located in the Entrada Sandstone in Arches National Park, Grand County, southeastern Utah (1317 m elevation). A sparse pinyon-juniper community occurs on the predominantly eolian sandy alluvium outside the south-facing entrance. The entrance to the dry rock shelter is approximately 10 m high and 22 m wide (Fig. 1). Much of the interior is choked with large roof spall boulders; however, one can easily proceed horizontally about 13 m into the shelter. Packrat (*Neotoma*) middens are common throughout the site. Initial analyses of seven of the indurated (cemented) middens, radiocarbon dating 12,400 to 20,000 years before present (yr B.P.) (S. Sharpe, in progress), indicate that Pleistocene-age materials (limber pine [*Pinus flexilis*], Douglas fir [*Pseudotsuga menziesii*], and numerous microfauna) occur at the site.

The entrance to the alcove is somewhat flattened and cleared of rubble in spots; higher up into the shelter many of the small boulders and larger packrat middens have been assembled to form one- or two-tier, dry-laid walls. Sand is deflating outside the alcove and uncovering lithic debitage. Pottery is rare. Two unindurated packrat stick middens occur in the shelter: one small nest at the east side of the entrance, and one large midden occupying the back of the shelter. In both cases these middens contain numerous skeletal elements of large and small mammals. The dry environment outside the alcove and the protective nature of the shelter have permitted the preservation of various specimens of keratin tissue (horn and hoof) from herbivores. A vandal's pothole occurs near the midden at the entrance area. Just upslope from this hole, and under a boulder where packrat activity occurs, we recovered an artifact made from hornsheath.

We felt that the alcove and its deposit required additional analyses due to the remains of bighorn (*Ovis canadensis*) and bison (*Bison bison*), the excellent preservation of keratin, and the recovery of the horn artifact. Although bighorn lived in the region throughout the Holocene, they were reintroduced to the park in 1985. The chronological range of the bison is inadequately understood for the Colorado Plateau. Given the known occurrence of Pleistocene packrat middens, it was conceivable that the artifact was also of late glacial age. This is a report of the bighorn and bison remains and bison artifact recovered from Bison Alcove, Arches National Park.

PACKRAT MIDDEN

Packrats typically collect plant, rock, animal (dung, hair, keratin, and skeletal), and artifactual material from within a range of 30–100 m of their den. These materials are placed over the nest mainly for protective

---

[1] Quaternary Studies Program, Box 5644, Northern Arizona University, Flagstaff, Arizona 86011-5644

[2] Department of Geology, Box 6030, Northern Arizona University, Flagstaff, Arizona 86011-6030.

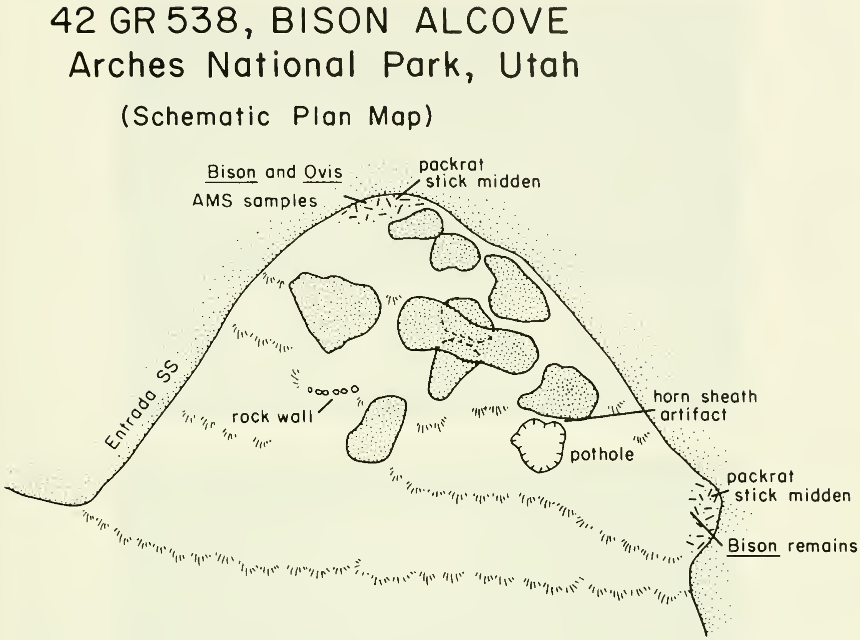


Fig. 1. Schematic plan map of Bison Alcove, Arches National Park.

construction. Often the packrat collects recently "living" materials, such as fresh plants, dung, and animal carcass remains. If the den construction is in a dry alcove in the hyperarid Southwest, the resulting midden will last as long as the shelter persists and represents the local biotic community at the time of collection (Betancourt et al. 1990). This same dry shelter may also preserve much older Pleistocene material, which the packrat may incorporate into a "recent" midden. Any item found loose in the dry alcove is "fair game" for a rummaging packrat.

The unindurated middens described above contained numerous bones of bighorn and bison. These materials could conceivably have been of late Pleistocene age, or they could be Holocene remains procured by local humans or packrats. The sample of large mammal bones was collected from the unindurated packrat midden in the back of the shelter; the artifact was collected from the surface near the front of the alcove. Due to the dry environment and continued preservation in the alcove spanning at least the past 20,000 years, precise age determination of the remains can occur only through direct radiocarbon dating.

FAUNAL REMAINS

Ovis canadensis

Bighorn remains were the most numerous large mammal remains in Bison Alcove. The following skeletal elements were recovered: horncore with sheath ($n = 1$) (Fig. 2A), axis (2; one burnt), thoracic vertebra (2), sacrum (2), scapula (1), tibia (1; distal fragment), metatarsal (1; distal fragment), and 2nd phalanx (1). Some of these remains exhibit tissue still adhering to the bone. Although no butchering marks are evident, the burning and the location of fragmentation could imply human usage. A minimum number of individuals (MNI) of two bighorn was represented, based on the sacrum.

The horncore remain, although fragmented and removed from the skull, was from a young

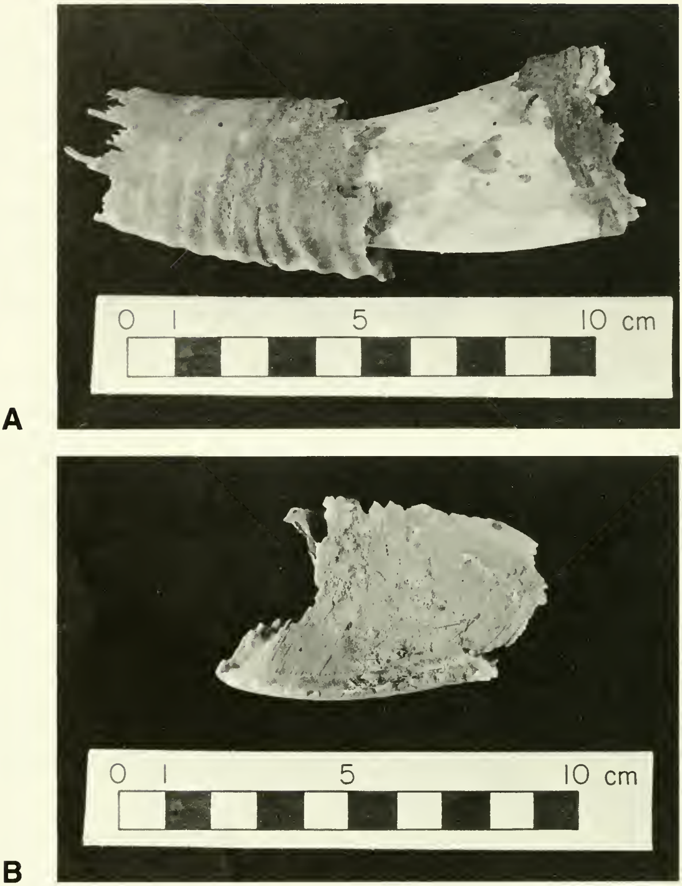


Fig. 2. Skeletal remains from the packrat midden: A, horncore and attached sheath of a young adult bighorn, *Ovis canadensis;* B, hoof remain of a young bison, *Bison bison*. Samples of keratinous tissue were removed from each specimen for AMS radiocarbon dating.

adult, possibly a female, based on the amount of internal core ossification and the length cross-section shape of the core and sheath. The unburned axis shows extreme degradation due to prolonged exposure to sun and possibly moisture. This bone was probably collected by the packrat from either outside the shelter or from the dripline area.

Bison bison

Bison remains were found throughout the shelter, but never in great quantity. The following skeletal elements were recovered (Fig. 2B): hornsheath (1; fragment constructed into artifact), centrum plate (2), ulna (1; proximal fragment), 1st phalanx (1), 2nd phalanx (3), 3rd hoof phalanx (3), and keratin hoof (1). No butchering marks were observed on any of these bones, although evidence of rodent gnawing was common. There appears to be an MNI of one bison. The size of the terminal phalange, the unfused centrum vertebral plates, and the hollow length versus the diameter of the hornsheath suggest that the bison was a young adult.

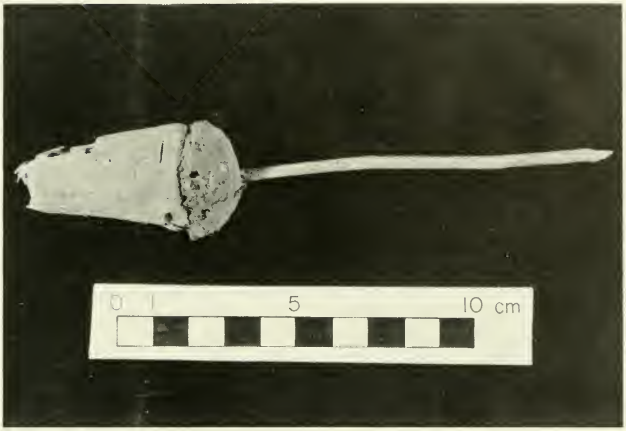


Fig. 3. Artifact made of bison hornsheath and pine pitch. Dermestid beetle chewing can be seen at the left end and top of the hornsheath. A knife cut mark is seen near the basal edge of the sheath adjacent to a circular groove used to cut the sheath from the horncore.

ARTIFACT DESCRIPTION

The artifact contains three parts: hornsheath, twig, and resin (Fig. 3). The total length is 163 mm, the hornsheath 50 mm, resin 16 mm, and protruding twig 97 mm. The hornsheath base is straight and contains a hollow center, indicating that it was cut from the burr and horncore of the bison skull. An isolated cut mark is seen above the base of the hornsheath (Fig. 3). The hornsheath now shows the burrowing damage of dermestid beetles; furrowing can be seen on the top edge of the sheath in Figure 3 and along the tip. It cannot be stated whether the tip of the horn was present when the artifact was constructed because it has since been consumed by beetles. Although it is possible that a human used an older, beetle-eaten hornsheath, the radiocarbon dates (see below) do not confirm this idea.

The resin is pine (*Pinus*) pitch; juniper (*Juniperus*) does not produce pitch in quantity. Most pitch exudes predominantly from a wound to the tree and stays malleable for approximately one to two years, after which it crystalizes (M. Wagner, Northern Arizona University). Pitch balls are preserved under trees in arid climate, such as in Arches National Park, and potentially can last for hundreds of years in the right environment.

A scenario of construction of the artifact follows: (1) The human procures a bison hornsheath. (2) Pine resin is pushed and molded into the base of the hollow (natural) hornsheath. (3) A twig of unknown identification is pushed into the soft resin before it hardens.

The function of this artifact is not understood; it would be pure speculation to identify this object as a "religious device," a tool, or a child's toy. A search through the Southwestern archaeological literature has failed to locate any examples of objects similar to this bison artifact. Morris (1980) illustrates a corn (maize) cob that contains a stick in one end and a feather inserted into the other end. The appearance is vaguely similar to our bison artifact. Morris (1980:139) states that these corn artifacts "may have been game darts, prayer sticks, or other ceremonial material" belonging to the Basketmaker people in the Prayer Rock district (tree-ring dating between A.D. 446 and A.D. 676), at the north end of the Lukachukai Mountains, Arizona.

RADIOCARBON DATING

Four samples were submitted for radiocarbon dating using the accelerator mass spectrometer (AMS) technique. All radiocarbon analyses were conducted by Beta Analytic Laboratories (Gainesville, Florida). A keratin hornsheath of *Ovis canadensis* and the isolated keratin hoof of *Bison bison* were selected from the unindurated midden located in the back of the alcove to provide direct dates on these species. Milligrams of keratin of each species were used in the analyses.

The bison artifact was dated twice using two different segments of the specimen (hornsheath and resin). Initially it was assumed that the hornsheath could be of late Pleistocene age, based on other Pleistocene plant and animal remains preserved within the packrat middens and the alcove; but the artifact could have been manufactured at a much later time. We assumed that dating the sheath would provide a time for the species presence at the alcove, and the analysis of the resin would determine the age for the manufacture of the artifact.

Figure 4 provides the radiocarbon age plus two standard deviations for each of the AMS dates. Uncorrected ages span a time, at two standard deviations of the mean, from A.D. 1180 to A.D. 1715 (720 to 235 yr B.P.). The radiocarbon ages illustrated in Figure 4 indicate that three of the dates are statistically the same age at one standard deviation of the mean (*Ovis* hornsheath, *Bison* hoof, and the *Bison* hornsheath). The resin in the artifact is older than the other three, but it is within a single grouping at two standard deviations. There are two scenarios for the use of the radiocarbon dates: (1) Group all four dates together at two standard deviations and determine the co-occurence age. (2) The resin is actually an "old pitch ball" (see above) by a hundred years or so, and therefore the actual age of the remains is best determined by omitting the resin date and calculating the co-occurrence age at one standard deviation of the mean for the three youngest dates.

All dates can be considered a single event in time (at two sigmas), having occurred between A.D. 1425 and A.D. 1490 (stippled area in figure; scenario 1). Holocene radiocarbon dates should be calibrated because of temporal variations in the radiocarbon content of atmospheric carbon dioxide. Numerous calibration techniques occur (including Ralph and Michael 1970, Stuiver and Reimer 1986). At the 95% confidence level using the calibration technique of Klein et al. (1982), our four dates fall within a time span of A.D. 1280 to A.D. 1650. A grouped overlap area within this calibration implies a possible single co-occurrence between A.D. 1405 and A.D. 1420 (Fig. 4). A high-precision calibration of the radiocarbon dates and a grouped overlap of corrected ages still implies a time of procurement and manufacture within the A.D. 1400s (Stuiver and Pearson 1986).

Scenario 2 is also depicted in Figure 4. By omitting the resin date, the co-occurrence age at one standard deviation is from A.D. 1535 to A.D. 1605, providing the implication that the bison, bighorn, and artifact were all utilized during the early historic period. Either scenario is reasonable to pursue.

DISCUSSION AND CONCLUSIONS

The question arises as to whether or not the bison remains were locally procured, either by humans or packrats, or brought to the alcove as a traded or long-distant-hunted carcass; i.e., were bison present in Arches National Park in A.D. 1400 to A.D. 1600? One way to attempt to answer the question is to examine the represented bison bones. Wheat (1972:101) states that

> . . . virtually all sources, both historic and ethnographic, concur in listing the choicest parts of the bison as the tongue, hump ribs with meat, marrow bones, and ribs, in about that order.

It is implied that if only these bones are recovered from a site, it can be assumed that the bison was brought into the area by trade for "choicest" meat parts (Wheat 1972, Driver 1990). Had the carcasses been locally procured, more of the animal (e.g., phalanges, pelvic region, etc.) would be recovered.

The list of bison bones presented here is biased in two ways. First the sample of bones is a grab sample of the bones we saw in the unindurated packrat midden. We did not systematically sample all the bones from the midden. Second, the bones represented in the midden are of the size that can be carried by a packrat. A bighorn radius, metapodial, or single mandible is about the maximum size and weight of bones observed to be carried by the largest packrat species (bushy-tailed packrat, *Neotoma cinerea*); this packrat presently inhabits the alcove. Marrow-containing bones (humerus, tibia, femur), if present in Bison Alcove, most likely would not have been incorporated into the midden by the packrat due to their large size.

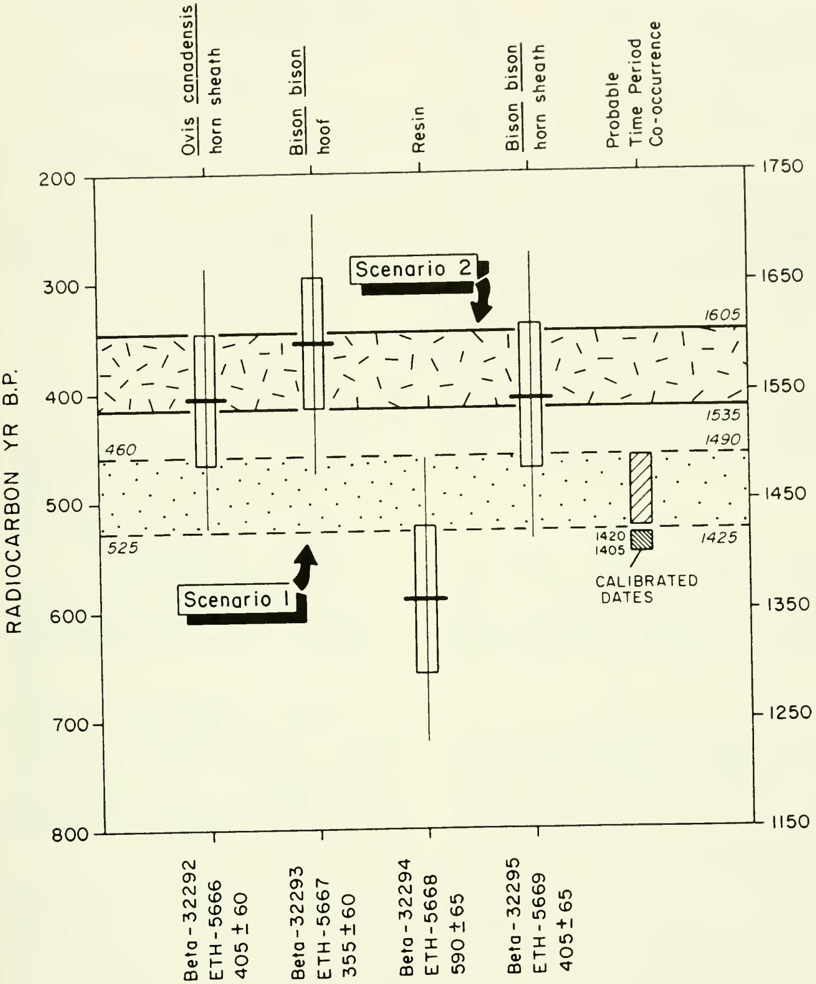


Fig. 4. Graph of the AMS radiocarbon dates from the bighorn and bison skeletal and artifact remains. Laboratory numbers and actual radiocarbon date are at the bottom. Material dated is at the top. One (box) and two (vertical line) standard deviations of the date (horizontal line) are shown for each date. See text for discussion.

These biases should not affect our determination of whether or not the bison was locally procured. We did recover some leg elements (phalange and ulna), some vertebral elements (unfused centrum plates), and a fragment representing the skull. Although the hornsheath could have been traded, the other elements are not from the "choicest parts." We therefore feel that the young bison must have been a local community inhabitant.

It is possible that bison, albeit rarely to occasionally, roamed through Arches National Park during A.D. 1400s to A.D. 1600s. One could have died near Bison Alcove, and only the packrat-size portions were collected by *Neotoma* and carried back to the shelter. What appears more likely, given the construction of the bison hornsheath artifact, is that a bison was procured (scavanged or hunted) near the alcove by humans. The bison carcass was rendered outside the alcove, and the "choicest parts" were either carried away from the site for later consumption or consumed at the site, with the larger bones later scattered by carnivores. The small-element bones were taken by the packrat and placed into its midden at the back of the alcove.

Bison are well documented as having lived in a wide variety of habitats on the Colorado Plateau during the late Pleistocene (Lindsay and Tessman 1974, McDonald 1981, Mead and Agenbroad 1989). The Holocene record of *Bison* on the Colorado Plateau is less well understood, but they were present at least rarely during protohistoric times.

ACKNOWLEDGMENTS

All specimens are curated and archived at Northern Arizona University, in the National Park Service repository, Quaternary Studies Program. Bruce Louthan (Bureau of Land Management, Utah), Chas Cartwright (Hovenweep National Monument, Colorado), Harvey Wickware (Canyonlands National Park, Utah), and Dave Eddy, Damian Fagan, Paul Guraedy, John McLaughlin, and Kim Tennyson (Arches National Park, Utah) helped with various logistics. Bax Barton, Mark Lawler (Quaternary Studies Program, Northern Arizona University), and Bruce Huckell (Arizona State Museum) helped with editing and researching the manuscript. Work was conducted under National Park Service contract CX-1200-4-A062. Emilee Mead provided drafting and photography.

LITERATURE CITED

BETANCOURT, J. L., T. R. VAN DEVENDER, AND P. S. MARTIN. 1990. Packrat middens; the last 40,000 years of biotic change. University of Arizona Press, Tucson.

DRIVER, J. C. 1990. Bison assemblages from the Sierra Blanca Region, southeastern New Mexico. Kiva 55:245–263.

KLEIN, J., J. D. LERMAN, P. E. DAMON, AND E. K. RALPH. 1982. Calibration of radiocarbon dates. Radiocarbon 24:103–150.

LINDSAY, E., AND N. TESSMAN. 1974. Cenozoic vertebrate localities in Arizona. Journal of the Arizona Academy of Science 9:3–24.

MCDONALD, J. N. 1981. North American bison: their classification and evolution. University of California Press, Berkeley.

MEAD, J. I., AND L. D. AGENBROAD. 1989. Pleistocene dung and the extinct herbivores of the Colorado Plateau, southwestern USA. Cranium 6:29–44.

MORRIS, E. A. 1980. Basketmaker Caves in the Prayer Rock district, northeastern Arizona. Anthropological Papers of the University of Arizona No. 35. University of Arizona Press, Tucson.

RALPH, E. K., AND H. N. MICHAEL. 1970. MASCA radiocarbon dates for sequoia and bristlecone pine samples. Pages 619–624 *in* I. U. Olsson, ed., Radiocarbon variations and absolute chronology. Nobel Symposium, 12th proceedings. John Wiley & Sons, New York.

STUIVER, M., AND G. W. PEARSON. 1986. High-precision calibration of the radiocarbon time scale, AD 1950–500 BC. Radiocarbon 28:805–838.

STUIVER, M., AND P. J. REIMER. 1986. A computer program for radiocarbon age calibration. Radiocarbon 28: 1022–1030.

WHEAT, J. B. 1972. The Olsen-Chubuck site: a Paleo-Indian bison kill. Society of American Archaeology Memoir No. 26. Washington, D.C.

Received 20 March 1991
Accepted 19 August 1991

Great Basin Naturalist 51(4), 1991, pp. 343–347

RADIO HARNESS SYSTEM FOR BOBCAT KITTENS

Boyde H. Blackwell[1], Grant T. Frost[1], Jerran T. Flinders[1], and Harry A. Barber[1]

ABSTRACT.—Eight bobcat kittens were fitted with a specially designed harness system supporting a radio transmitter. These kittens were the youngest known to be radio-instrumented. This system was used successfully through two seasons, from June 1989 to January 1991. Litters of kittens were located soon after birth for weighing, marking, and aging (by tooth eruption). During the first year when kittens were at least eight weeks old and six weeks old the second year, attempts were made to radio-instrument kittens in each litter. This harness system allowed litters to be located periodically until their death or dispersal. We were able to collect important data during the most crucial and least known weeks of the lives of bobcat kittens.

Key words: bobcat, Felis rufus, *kitten, radio telemetry, behavior, mortality, break-away harness, Utah.*

Little information has been generated concerning the first 48 weeks of life for bobcat kittens (*Felis rufus*). McCord and Cardoza (1982) and Jackson (1986) reported these first weeks of life were crucial to further development of hunting and predator-avoidance skills that enable the dispersal of experienced bobcat kittens. Our study of bobcats made it increasingly clear that habitat selection, location of prey, location of fresh water, and successful predator avoidance are all important factors directly related to survival of bobcat kittens.

Radio-instrumented collars have been used successfully to collect data on bobcats in many areas (Bailey 1974, Karpowitz 1981, Lawhead 1984, Jackson 1986, Litvaitis et al. 1986). However, due to the rapid growth of bobcat kittens in their first year, the fixed collar used for adult bobcats was not considered an option. Intraperitoneal-implanted transmitters were also not considered a safe option for kittens for fear that in recovering from surgery they would not be able to keep up with the normal movements of the litter and might have difficulty competing for food. Jackson et al. (1988) developed an expandable, drop-off harness for bobcat kittens five months or older, which he used in Colorado.

After our first year of study concerning the reproductive habits of female bobcats and their young in Utah, we felt it necessary to develop a radio-instrumented harness that would fit smaller and younger kittens yet expand to fit juveniles. By modifying Jackson et al.'s (1988) design, we were able to develop a harness successfully used on bobcat kittens as young as six weeks old.

This study tested the hypotheses (1) that an expandable, drop-off, radio-instrumented harness could be successfully used on bobcat kittens as young as six weeks old and (2) that the harness would neither alter normal behavior nor contribute significantly to mortality.

STUDY AREA

The Sheeprock and Tintic mountains of the Wasatch National Forest and adjacent private property, as well as lands administered by the U.S. Bureau of Land Management, were established by the Utah Division of Wildlife Resources as a study area in 1987. Most of the area is closed to all harvest and pursuit of bobcats. Included are portions of Tooele and Juab counties in northwest central Utah. Sagebrush–desert shrub, pinion-juniper, mountain brush, and montane mixed forest are the common vegetative zones (Johnson 1989). Average annual precipitation ranges between 15.2 and 25.1 cm, with amounts increasing with elevation. Elevations range from about 1600 m to 2827 m. These mountains are typical of the cold-desert portion of the northern Great Basin.

---

[1] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

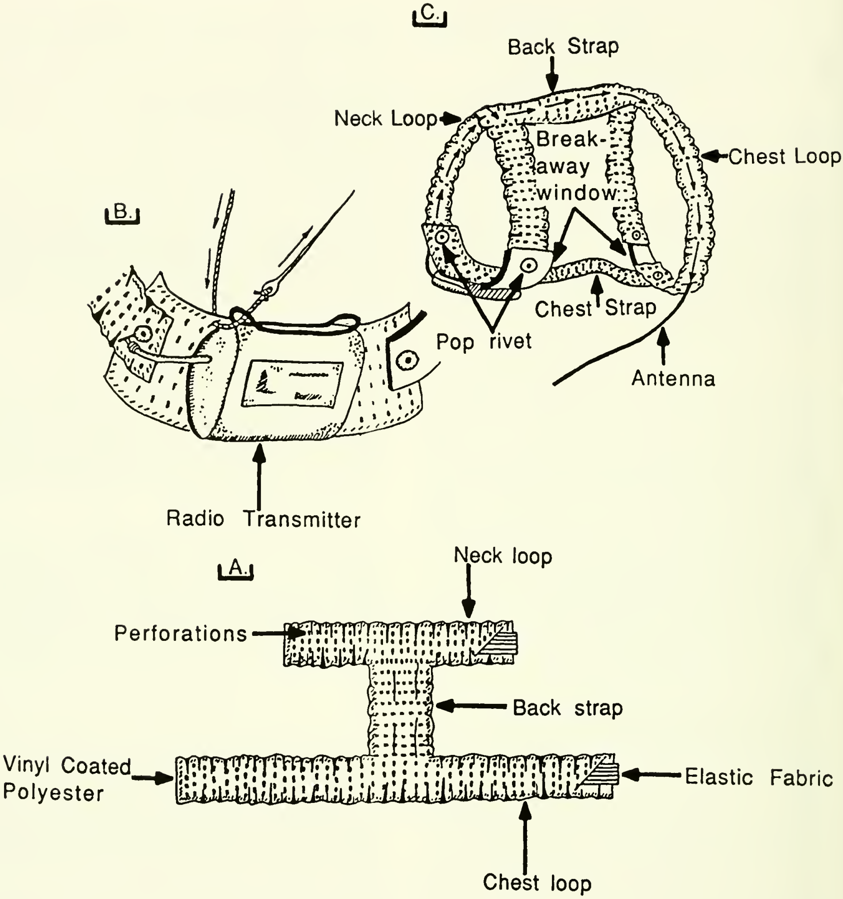

C.
Back Strap
Neck Loop
Break-away window
Chest Loop
Chest Strap
Pop rivet
Antenna
B.
Radio Transmitter
A.
Neck loop
Perforations
Back strap
Vinyl Coated Polyester
Elastic Fabric
Chest loop

Fig. 1. An expandable, drop-off, radio-transmitter harness constructed for use on kittens at least six weeks old. (A) One-piece harness with elastic fabric before harness was assembled. (B) Attachment of radio transmitter to neck loop. (C) Completed harness; neck and chest loops are 1.5 cm wide and elastic fabric is encased in vinyl-coated polyester (VCP). Neck loop expands from 15.5 to 26 cm, chest loop from 24 to 54 cm. Back strap (3 cm long × 2 cm wide) and chest strap (6 cm long × 1.5 cm wide) are made of VCP. Antenna is encased by two sandwiched layers of VCP.

HARNESS CONSTRUCTION

Neck and chest loops, constructed of 1.3-cm-wide elastic fabric, were completely covered by a layer of brown vinyl-coated polyester (VCP) reinforced with imbedded woven nylon string (Fig. 1A). VCP is a perforated fabric and allows sunlight to penetrate to the rubber fabric, thus increasing potential for time-based disintegration. These perforations are approximately 2 mm × 1 mm (10 per 1 cm^2). Neck and chest loops, as well as the back strap, were constructed in one piece in the shape of a capital H (Fig. 1A).

The VCP chest strap was pop-riveted to the chest loop and sewn to the neck loop with waxed upholstery cord. A small radio transmitter (Telonics Inc. Model 070, Mesa, Arizona) was stitched, with waxed upholstery cord, to a wider piece of VCP fabric inserted at the bottom of the neck loop (Fig. 1B). The antenna for the transmitter, encased in the VCP harness, protruded slightly from the chest loop at the bottom (Fig. 1C). The edges of the VCP harness were double stitched with nylon thread. The completed width of the chest and neck loops was 1.5 cm, the back strap was 2 cm wide × 3 cm long, and the chest strap was 1.5 cm wide × 6 cm long.

The neck loop circumference was 15.5 cm and expanded to 26 cm, while the chest loop was 24 cm and expanded to 54 cm. The average weight of the completed harness system was 46.5 g, less than half the weight of the harness used by Jackson et al. (115 g; 1988).

RESULTS

To place the harness on the bobcat kitten, we stretched and pulled the neck and chest loops over the bobcat's head. The neck loop rests in front of the shoulders on the neck, with the transmitter under the chin (Fig. 2A). The chest loop fits behind the front legs, with the legs straddling the chest strap (Fig. 2B).

We radio-instrumented eight bobcat kittens (four males, four females) (Table 1). One male kitten harnessed at nine weeks wore the harness system for 28 weeks, at which time the harness was replaced with a regular one-piece collar worn by other adult bobcats. We found the harness in very poor condition, as we had expected. We estimated that the harness would have fallen off in approximately three to four more weeks. There were no abrasions or sores caused from wearing it.

The harnesses were worn by the kittens for a varied number of days (Table 1), the least being two days, the most 32 weeks. One kitten was able to free itself from the harness because elastic inside the VCP was purposefully cut when the harness was first placed on the kitten. One kitten apparently hooked the back strap on a branch of a prostrate juniper tree and in its struggle to free itself twisted the harness tighter around the branch and its neck.

DISCUSSION

Only one kitten, which wore the harness for 32 weeks, was found to have harness-related sores present on the neck and in the chest loop area. Because of this, we added two break-away windows (Fig. 1C) to the neck and chest loops, factors that will greatly increase the probability that the harness will break away before causing abrasive injury to the kitten.

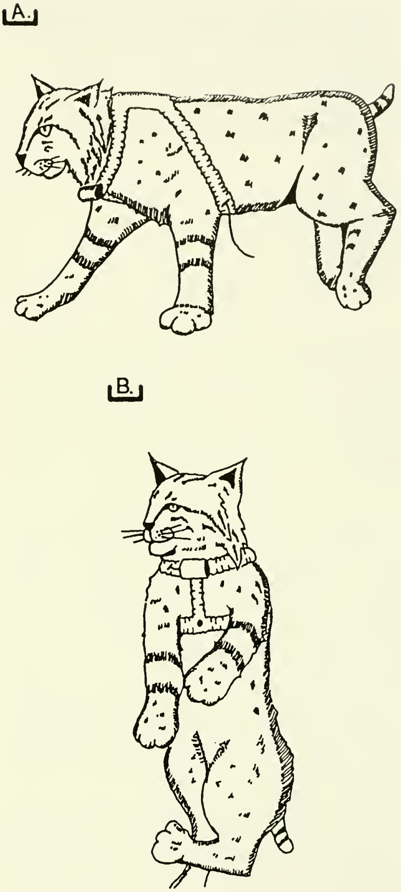


Fig. 2. (A) Side view of bobcat kitten wearing harness. (B) Bottom view of harness worn by bobcat kitten with front legs on either side of chest strap.

Steigers and Flinders (1980) developed a break-away, expandable collar for mule deer fawns. We recommend this same type of break-away system for the bobcat kitten harness to ensure a complete and timely loss of the harness. Steigers and Flinders found

TABLE 1. Results of radio-instrumented harness system fitted to eight bobcat kittens, 1989–1990.

Bobcat kittens	Age (weeks)	Weight (g)	Harness use (weeks)	Results
17M male	9	1600	28/replaced	dispersed
22M male	18	3200	13	death/starvation
24F female	14	1900	16	death/predation
29F female	8	1480	4	radio stopped
30F female	8	1210	2 days	slipped harness
33M male	6	1100	7	death/natural
34F female	6	1050	3	death/harness
35M male	9	1610	32	collar broke away

that surgical tubing (0.318-cm wall thickness × 1.27-cm diameter) had an approximate life of 10–13 months and recommended thinner tubing for shorter life. We recommend 0.159-cm-thick tubing and are confident that this addition will meet our objectives for future use.

We have found that valuable data can be collected on mortality rates and behavior of young bobcats with this harness system. Not counting the harness-related death, there was a high natural mortality rate for the kittens. Two of the seven died of natural causes while wearing the harness. Two that grew large enough to wear adult radio collars were lost as juveniles: one died of starvation or disease, and the other disappeared during dispersal. Our data show there is a high mortality rate at all stages for young bobcats (Table 1).

By taking simultaneous readings of locations for collared dam bobcats and offspring with harnesses (and in one case between two siblings harnessed at the same time), we were able to study patterns of movement, home-range use, and family continuity. All kittens had a lower average daily minimum movement than their dams, confining their activities almost exclusively to the core area of the dams' home ranges (determined with Program Home Range, Ackerman et al. 1989). Kittens were found up to 1.5 km apart, but one would be with the mother and the other in a secure den. The mother was located with at least one of her kittens 50–80% of the time. When the mother was not with the kittens, she was found up to 2 km away. This suggests that estimates of kitten survival may not be very accurate if based on observations of kittens seen with their dams.

ACKNOWLEDGMENTS

The major funding for this project was provided through the U.S. Fish and Wildlife Service, Utah Division of Wildlife Resources, and Brigham Young University; additional assistance was provided by the Utah Chapter of The Wildlife Society. We thank the U.S. Forest Service, Bureau of Land Management, and the U.S. Army at Dugway Proving Grounds, Tooele County, Utah, for equipment and residency during the study. We also acknowledge private landholders for allowing access to their land. We thank Earl Southerland, our trapper and houndsman, and the Utah Division of Wildlife Resources nongame managers Randy Radant, Jordan Pederson, Kenneth McDonald, Dennis Shirley, and Bill Bates for their dedicated support. We also appreciate the Brigham Young University Upholstery Department for providing counsel and workmanship on the kitten harnesses.

LITERATURE CITED

ACKERMAN, B. B., F. A. LEBAN, M. D. SAMUEL, AND E. O. GARTON. 1989. User's manual for program home range. 2nd ed. Technical Report 15. Forestry, Wildlife and Range Experiment Station, University of Idaho, Moscow. 79 pp.

BAILEY, T. N. 1974. Social organization in a bobcat population. Journal of Wildlife Management 38: 435–446.

JACKSON, D. H. 1986. Ecology of bobcats in east-central Colorado. Unpublished dissertation, Colorado State University, Fort Collins. 116 pp.

JACKSON, D. H., L. S. JACKSON, AND W. K. SEITZ. 1988. An expandable drop-off transmitter harness for young bobcats. Journal of Wildlife Management 49: 46–49.

JOHNSON, KENDALL L. 1989. Rangeland resources of Utah. A cooperative service of Utah State University, Logan, Utah. Utah Rangeland Committee. 103 pp.

KARPOWITZ, J. T. 1981. Home ranges and movements of Utah bobcats with reference to home range selection and prey base. Unpublished thesis, Brigham Young University, Provo, Utah. 42 pp.

LAWHEAD, D. N. 1984. Bobcat (*Lynx rufus*) home range, density and habitat preference in south-central Arizona. Southwest Naturalist 29: 105–113.

LITVAITIS, J. A., J. T. MAJOR, AND J. A. SHERBURNE. 1986. A status report: bobcat movements in relation to snowshoe hare density. Page 375 *in* S. D. Miller and D. D. Everett, eds., Proceedings of International Symposium, 1982, College of Agriculture, Texas A & I University, Kingsville.

McCORD, C. M., AND J. E. CARDOZA. 1982. Bobcat and lynx. Pages 728–766 *in* J. A. Chapman and G. A. Feldhamer, eds., Wild mammals of North America. Johns Hopkins University Press, Baltimore, Maryland.

STEIGERS, W. D., AND J. T. FLINDERS. 1980. A break-away expandible collar for cervids. Journal of Mammalogy 61: 150–152.

Received 1 May 1991
Accepted 1 August 1991

Great Basin Naturalist 51(4), 1991, pp. 348–376

FLOWER MITES OF TRINIDAD II. THE GENUS *PROCTOLAELAPS* (ACARI: ASCIDAE)

Barry M. OConnor[1], Robert K. Colwell[2], and Shahid Naeem[1]

ABSTRACT.—Nine species of mites of the genus *Proctolaelaps* were collected in flowers or phoretic in the nares of hummingbirds in Trinidad. Previously named species *P. kirmsei*, *P. glaucis*, and *P. belemensis* are redescribed, and six new species are described: *P. jurgatus*, *P. mermillion*, *P. rabulatus*, *P. contumex*, *P. certator*, and *P. contentiosus*. *Proctolaelaps belemensis cyanocompsae* is raised to specific status. Host plants are given for all species except *P. mermillion*, which was collected only from a hummingbird host. New World flower-inhabiting *Proctolaelaps* are grouped into two hypothetically monophyletic lineages, the *kirmsei*-group and the *belemensis*-group, on the basis of adult morphology. A key to the nine Trinidadian species is given.

Key words: Trinidad, flower mite, Proctolaelaps, *Ascidae, hummingbird.*

Mites of the family Ascidae are common inhabitants of flowers in tropical and subtropical regions of the New World. Most of these flower-inhabiting species disperse through phoretic association with hummingbirds, although some have been collected from other bird groups and from Lepidoptera. The mites are typically carried in the nares of the bird. This is the second report on the systematics of these mites based on studies carried out on the island of Trinidad during the years 1975–1982 by field teams led by one of us (RKC). Three genera of Ascidae include species exhibiting flower-bird associations. We have previously reported on the two Trinidadian species belonging to the predatory genus *Lasioseius* (Naeem et al. 1985). This paper will deal with species of the genus *Proctolaelaps*, while the third genus, *Rhinoseius*, will be considered in a final report (OConnor et al., in preparation).

Species of *Proctolaelaps* have been described from flowers in Africa (Ryke 1954, 1964) and from nectarivorous vertebrates from Australia (Domrow 1979). Fain et al. (1977a) first reported *Proctolaelaps* from the nares of hummingbirds from the New World, briefly describing four new species: *P. hunteri*, *P. kirmsei*, *P. glaucis*, and *P. belemensis*. Those authors later (Fain et al. 1977b) gave more complete descriptions of these species and described a new subspecies, *P. belemensis cyanocompsae*, from the nares of a cardinaline finch, *Passerina* (=*Cyanocompsa*) *cyanoides*. Hyland et al. (1978) gave new host and locality records for *P. kirmsei* and *P. belemensis* and described two new species, *P. mexicanus* and *P. spiralis*, the former from the nares of a tanager, *Euphonia hirundinacea*.

Fain et al. (1977b) noted that all of the New World bird-phoretic *Proctolaelaps* shared certain unique morphological characteristics, notably the reduced cheliceral dentition and the presence of a large ventral spurlike seta on femur IV of the male. These characteristics are also found in the Australian species *P. spencerae* Domrow, 1979, but not in the African flower-inhabiting *P. vandenbergi* and *P. proteae* (Ryke 1954). Fain et al. (1977b) regarded the systematic position of the hummingbird-associated *Proctolaelaps* as uncertain, noting,

> We have placed all these species in the genus *Proctolaelaps* but it is quite possible that some or all belong to another perhaps undescribed genus intermediate between *Rhinoseius* and *Proctolaelaps* (p. 127).

In his recent revision of *Proctolaelaps*, Karg (1985) made no mention of any of these New World or Australian species. In his taxonomic arrangement, in which subgenera and species groups were based on single character differences, all of the flower-inhabiting species would belong to the *pygmaeus* species group of the subgenus *Proctolaelaps* (sensu stricto).

---

[1] Museum of Zoology and Department of Biology, University of Michigan, Ann Arbor, Michigan 48109.

[2] Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3042.

It might appear that the character states noted above that are shared by the New World flower-inhabiting *Proctolaelaps* and the Australian *P. spencerae* are synapomorphies, suggesting a common ancestry. However, some caution is necessary before accepting this conclusion. It should be noted that similar character states (i.e., reduced cheliceral dentition and spurs on male femora IV) are found in the ameroseiid genus *Hattena*, a genus known previously only from the nares of nectarivorous birds (Meliphagidae) from Australia (Domrow 1979). We have obtained specimens of *Hattena cometis* Domrow, 1979, from flowers of *Castanospermum australle* in Sydney, Australia, verifying that these mites are ecologically similar to the New World flower mites. Reduction in cheliceral dentition appears to be correlated with the switch from predation to nectar-feeding in ascid and ameroseiid mites. Similarly, male armature is a correlate of the agonistic behavior exhibited by males toward each other (Colwell 1979, 1985, 1986a). Given the obvious convergence in morphology between flower-inhabiting *Proctolaelaps* and *Hattena*, the monophyly of the flower inhabiting *Proctolaelaps* of Australia and the New World must be tested using additional characters.

The New World flower-inhabiting *Proctolaelaps* that we have examined can easily be separated into two hypothetically monophyletic groups, the "*kirmsei*-group," and the "*belemensis*-group." These species groups are diagnosed below.

Observations on the ecology, behavior, and host associations of flower-inhabiting *Proctolaelaps* have been given by Colwell (1979, 1985, 1986a, 1986b), Dobkin (1984, 1985), and Heyneman et al. (1990). Because completion of our taxonomic studies on the Trinidad flower mites has lagged behind publication of ecological and behavioral studies, some species names have previously appeared as nomina nuda (Dobkin 1985, Colwell 1986a, 1986b, Heyneman et al. 1990). These names are validated here.

METHODS AND MATERIALS

Field studies were carried out during the period 1975–1982 at a variety of sites in Trinidad's Northern Range. The range consists of several parallel mountainous ridges that form valleys oriented primarily in a north-south direction. The mountains reach about 1000 m in height. From east to west, the principal valleys from which our collections were made are the Arima, Guanapo, Aripo, and Oropuche valleys. The last contains localities from which mites had been previously collected by T. H. G. Aitken from 1954 to 1966 (Fain et al. 1977b). Most of our collecting efforts were concentrated in the Arima Valley along the Arima and Blanchisseuse roads; the latter runs through the Northern Range to the north coastal town of Blanchisseuse. Many collections were made near the Simla Research Station, owned and operated by the Asa Wright Nature Center, at 200 m elevation in the Arima Valley. The habitat is humid montane seasonal tropical rain forest with annual rainfall of 100–250 cm. The dry season occurs from January to April, the wet season from May until December. Although there are several government-managed forest reserves in the Northern Range, pristine or mature areas of forest are rare. Our collection sites were often in these forest reserves, which were largely secondary growth or under cultivation by individual farmers. Agricultural methods include slash-and-burn techniques, and during dry years extensive areas of the valleys are burned. The most disturbed areas occurred in the eastern valleys.

Most of the hummingbird-pollinated plants from which mites were collected (all indigenous species) thrive in secondary and disturbed habitats. Our collections from host plants and from birds were therefore primarily from roadsides, disturbed habitats bordering small farms, and secondary tropical rain forest. Few collections were made in mature rain forest. One additional collecting locality, Waller Field, lies 11.6 km southeast of the Simla station. This site was once a lowland (30 m) tropical rain forest but is largely secondary habitat now. A few patches of rain forest persist there, but the area is mostly young trees, shrubs, and herbs. This area, an abandoned military air field, is favorable for many of the species of plants harboring flower mites. Further descriptions of the habitats can be found in references in Dobkin (1985).

In the field, flowers or flower bracts were removed from the plant and placed in individual vials of 70% ethanol. Additional specimens were collected from hummingbird hosts by capturing the birds in mist nets and aspirating the mites from the nares. Birds were identified and released. Mites were cleared and mounted in Hoyer's medium in the laboratory.

Our specimens were compared with the holotypes of named species in the laboratory of Dr. Alex Fain in Antwerp, Belgium. It should be noted that the holotypes of species described by Fain et al. (1977a) were stated to have been deposited in the U.S. National Museum of Natural History in Washington. Through the courtesy of Dr. Fain, one of us (BMOC) was able to study these specimens in Dr. Fain's laboratory in 1983. According to Mr. Robert Smiley, Systematic Entomology Laboratory, USDA (personal communication, 1990) the specimens have not been received by the National Museum and are presumably still in the collection of Dr. Fain.

Types and voucher specimens from our studies are deposited in the following institutions: University of Michigan Museum of Zoology, Ann Arbor, Michigan (UMMZ); Life Science Museum, Brigham Young University, Provo, Utah (BYU); U.S. National Museum of Natural History, Washington, D.C. (NMNH); Canadian National Collection of Arthropods, Biosystematics Research Centre, Ottawa, Ontario, Canada (CNC); L'Institut Royal des Sciences Naturelles, Brussels, Belgium (IRSNB).

In the following descriptions, all measurements are given in micrometers (μm). For new species, measurements are given as follows: holotype, mean (range) (number of specimens measured). For the other sex and for previously described species, measurements are given as mean (range) (number of specimens measured). For each species, 10 individuals of each sex including individuals from all host plants were measured when available.

SPECIES ACCOUNTS

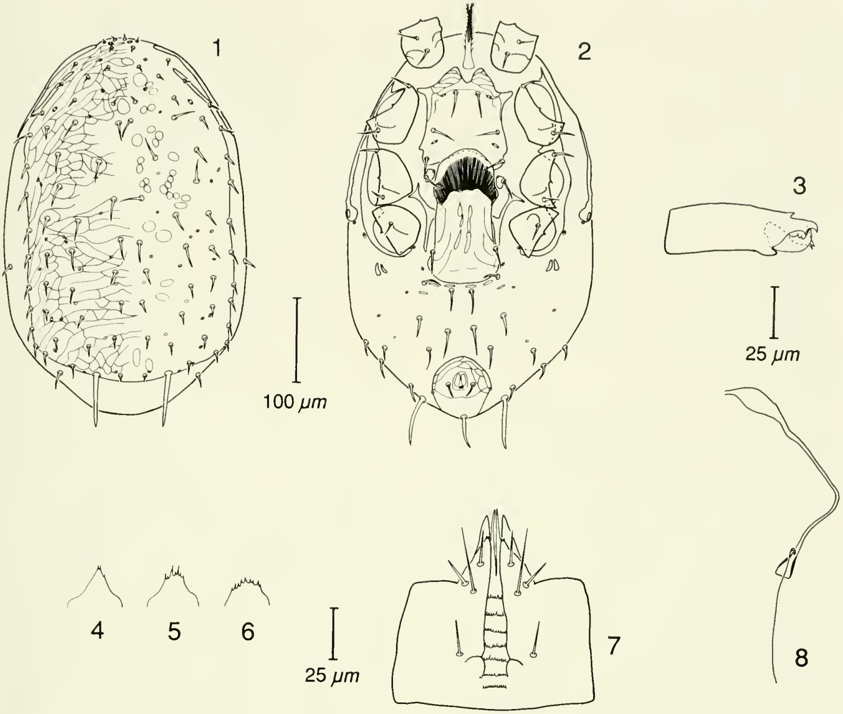
The *Proctolaelaps kirmsei* group

The *Proctolaelaps kirmsei* group may be diagnosed by the narrow rows of deutosternal teeth and the modification of certain leg setae in the male: the three ventral setae of femur II are enlarged and spinelike; the enlarged seta v of femur IV is partially fused to a cuticular projection of the segment; and setae av1–2, pv1–2, and mv of tarsus II, seta av1 of genu IV, and setae av1 and pv1 of tibia IV all share a unique structure. The bases of these setae are inflated ventrally, with the filiform part of the seta projecting from the base at an angle. Narrow deutosternal tooth rows occur in some nonflower-inhabiting *Proctolaelaps*, but the modifications of the male legs are unique synapomorphies not occurring in any other *Proctolaelaps* species. Modification of some setae of tarsus II in the male is known in the genus (e.g., *P. subcorticalis* Lindquist, 1971); however, the particular form of the setae in these flower mites is unique. Described species having this set of derived characters include *P. kirmsei* and *P. glaucis*. Published descriptions of *P. hunteri* and *P. mexicanus* mention or illustrate the partially fused seta and tubercle of femur IV and the spinelike setae ventrally on femur II, and mention the presence of "spines" on tarsus II, but the text and figures are not specific as to the form or homology of the "spines." We regard these species as also belonging to this group, pending reexamination of the tarsal setation. Five species belonging to this group were collected in Trinidad: *P. kirmsei*, *P. glaucis*, and three new species.

Proctolaelaps kirmsei **Fain,** Hyland and Aitken, 1977

- *Proctolaelaps kirmsei* Fain, Hyland and Aitken, 1977a: 185
- *Proctolaelaps kirmsei* Fain, Hyland and Aitken, 1977b: 131
- *Proctolaelaps kirmsei* Hyland, Fain and Moorhouse 1978: 263
- *Proctolaelaps kirmsei* Colwell, 1985: 59
- *Proctolaelaps kirmsei* Colwell, 1986a: 408
- *Proctolaelaps kirmsei* Colwell, 1986b: 485
- *Proctolaelaps kirmsei* Heyneman et al., 1990: 458

This species was briefly diagnosed from a male and a female specimen collected from the nares of *Phaethornis augusti* from Birongo, Venezuela (Fain et al. 1977a). Fain et al. (1977b) provided some additional measurements and a figure of the male. They noted that all female specimens were in poor condition. Hyland et al. (1978) reported a single female from *Phaethornis superciliosus* from Veracruz, Mexico. Detailed observations on the ecology and host-plant associations of this species in Trinidad have been presented by Colwell (1985, 1986a) and Heyneman et al. (1990). We give here a complete description and figures of both sexes based on our Trinidad material. Our specimens were compared with the holotype.



Figs. 1–8. *Proctolaelaps kirmsei*, female: 1, dorsum; 2, venter; 3, chelicera; 4–6, variation in tectum form; 7, subcapitulum, ventral view; 8, spermathecal system.

FEMALE (Figs. 1–8).—Idiosomal length 483 (450–509), width 308 (287–322); dorsal shield length 452 (410–486), width 276 (252–304) (*n* = 10). Dorsal shield (Fig. 1) with reticulate pattern over entire surface. Dorsal shield with 44 pairs of smooth, simple setae; marginal setae r2–r6 and R1–R6 on edge of shield, R7 on membrane posterior to shield; 3 pairs of submarginal setae (UR) on lateral membrane posteriad of coxae IV. The following measurements of dorsal setae were taken from the figured specimen, a mite of average body size: setae j1–4, z1–3, and s1–2 very short (7–11 μm), setae j5–6, z4–6, and s3–6 distinctly longer (22–29 μm), anterior marginal setae (r2–6) intermediate in length (13–18 μm); posterior half of shield with J1 (24 μm) longer than other setae, most of which are approximately 13 μm long, exceptions are the very short J5 (6 μm) and the large, stout Z5 (68 μm). Glands, proprioceptors, and muscle scars positioned as indicated in Figure 1.

Venter (Fig. 2) with tritosternum with elongate base and slender, tapering, pilose laciniae. Sternal shield longer than wide, with 3 pairs of setae and 2 pairs of pores, anterior lobes of shield well developed, with distinct linear pattern. Fourth pair of sternal setae and 3rd pair of sternal pores on metasternal platelets. Genital shield with linear ornamentation, shield slightly widened behind genital setae. Four to six small sclerites positioned directly posterior to genital shield. Endopodal apodemes distinct between epigynial shield and coxae III-IV; exopodal sclerites extending from between coxae I-II to behind coxae IV. Two pairs of small, elongate metapodal plates. Anal shield ovoid, longer than wide (average length 84 μm, width 76 μm), ornamentation confined to anterior two-thirds, postanal seta slender, about twice as long as paraanal setae. Posterior ventral region with 8 pairs of setae (Jv1–5, Zv1–3), Jv1 and Jv2 typically longer than other anterior setae, Jv5 stout and 60–70 μm long; posterior submarginal setae (UR) also typically visible ventrally (Fig. 2). Peritreme extending anteriad to a point approximating base of dorsal seta z1. Spermathecal system consisting of a broad, membranous pouch just inside external opening, connecting with an adductor canal approximately 90 μm long; a small, bell-shaped maturation pouch lies at juncture of adductor canal and the long, thin spermiduct (Fig. 8).

Gnathosoma with tectum variably shaped, ranging from triangular with few teeth to broad and strongly toothed (Figs. 4–6). Chelicera with fixed digit bidentate; movable digit also bidentate with strong distal hook; a large, membranous process bearing 2 distal teeth present on paraxial face (Fig. 3). Deutosterum with 7 transverse rows of denticles; anterior 6 rows connected; no rows widened (Fig. 7). Rostral setae simple, slender, with internal posterior rostral setae at least twice as long as external posterior rostral setae; capitular setae slender, simple. Corniculi parallel; internal malae very thin, extending to or slightly beyond tip of corniculi. Palps similar to other *Proctolaelaps* species.

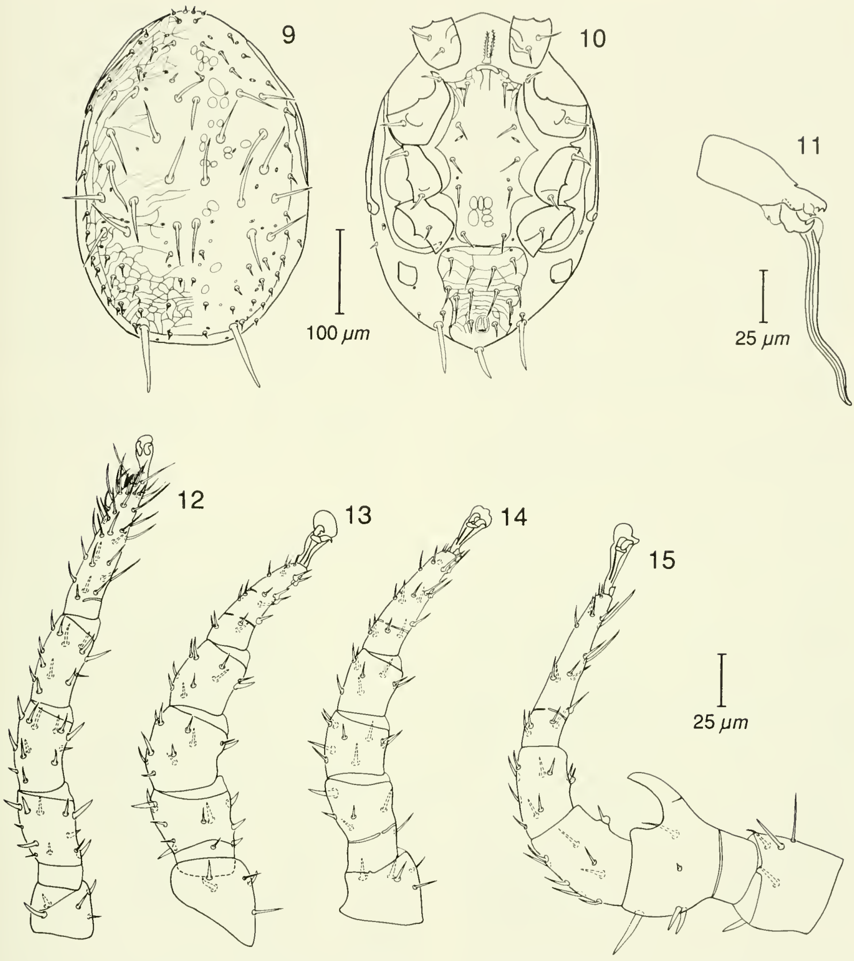
Legs I–IV (excluding pretarsi) 93, 73, 74, and 92% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxae II and III with pronounced convex boss, coxa IV with a weaker boss. Setation of genua of legs I, II, III, and IV, respectively, 13-11-9-9, that of tibia: 13-10-8-10; all leg setae setiform to filiform except the following spinelike setae: pd2 of femur II, ad1 of femur III, ad1 and ad2 of femur IV, and v of femur IV, which is strong and about as long as the segment width.

MALE (Figs. 9–15).—Idiosomal length 404 (382–422), width 281 (246–298) ($n = 10$). Reticulate pattern present on anterior and posterior quarters and laterally on shield, central half of shield with pattern very weak or absent (Fig. 9). Shield with 43–45 pairs of setae, posterior marginal (R) setae varying from 5 to 7 pairs, all on shield. One pair of submarginals (UR1) laterad of coxae IV. Anterior dorsal setae j1–4, z1–3, s1–2 very short (10–15 μm); central dorsal setae j5–6 and J1, z4–6 and Z1, s3–6 and S1 are strong spines 45–55 μm long; posterior dorsal setae (except Z5) also short (10–15 μm), Z5 is a thickened, blunt spine, 75–80 μm long; all marginal setae short. Glands, proprioceptors, and muscle scars as shown in Figure 9.

Venter (Fig. 10) with tritosternum with base distinctly shorter than in female. Sternogenital shield with reticulation confined to anteriolateral corners, smooth medially and posteriorly, with 5 pairs of setae and 3 pairs of pores. Metapodal plates quadrate, much larger than in female. Ventrianal shield relatively narrow, not extending to metapodal plates, reticulated over entire surface, with 5 pairs of ventral setae on shield, Jv1–3, Zv1–2, in addition to paraanal setae. Three pairs of ventral setae (Jv4, Jv5, and Zv3) on membrane. Setae Jv1, Jv2, Jv3, and Zv2 relatively long and setiform (28–35 μm), Zv1 setiform and somewhat shorter (21 μm); Jv4 and Zv3 microsetae (7–9 μm), and Jv5 a thick, blunt spine, 50–65 μm long. Paraanal setae approximately half as long as thick, blunt postanal seta (30–40 μm). Peritremes much shorter than in female, extending anteriad to the vicinity of seta s1. Endopodal apodemes fused to sternogenital shield; exopodal sclerites well developed laterad of coxae.

Gnathosoma with tectum simpler than in female, broadly rounded and with few or no teeth. Fixed digit of chelicera with one tooth and a bidentate, membranous process as in female; movable digit unidentate, with long, somewhat sinuous spermatodactyl projecting posterioventrally, 97–106 μm long (Fig. 11). Corniculi shorter and stouter than in female, widely spread basally; other features of gnathosoma as on female.

Legs I–IV (excluding pretarsi) 92, 77, 72, and 97% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxa II with pronounced convex boss, coxa III with a weaker boss, coxa IV without boss. Leg I generally similar to female except some setae of femur slightly more spinelike. Leg II distinctly thickened, setae ad1, pd2, and all three ventral setae in the form of thick spines; genu and tibia each with seta pv a thick spine; tarsus with setae av1–2, pv1–2, and mv with thickened, bulbous base. Leg III with setation generally similar to female but with



Figs. 9–15. *Proctolaelaps kirmsei*, male: 9, dorsum; 10, venter; 11, chelicera; 12, leg I, dorsal view; 13, leg II; 14, leg III; 15, leg IV.

tarsal setae av1–2, pv1–2, and mv modified as on leg II. Leg IV strongly modified; femur enlarged, with ventral apophysis bearing partially fused, spurlike ventral seta, dorsal setae thickened and spinelike, especially ad1; genu with ventral seta with bulbous base; tibia with ventral setae av and pv likewise modified; tarsus with seta mv with bulbous base, setae av1 and av2 distinctly longer than pv1 and pv2. Pretarsi relatively long.

MATERIAL EXAMINED.—The following specimens were examined from the listed host plants in Trinidad: ex *Hamelia patens* Jacques (Rubiaceae), Arima Valley, Davis Road near Temple Village, 27 August 1980, D. S. Dobkin (#96) (31 females, 17 males); same data (#90) (1 female); same data (#89) (3 females, 2 deutonymphs); Andrews Trace, 10 mi N Arima, 21 February 1976, R. K. Colwell (#U53) (4 females); same locality, 23 February

1976, R. K. Colwell (#U54) (1 male); ex *Palicourea crocea* (Sw.) R. & S. (Rubiaceae), Arima Valley, Temple Village, dirt road near Cricket Pitch, 21 February 1979, R. K. Colwell (#T248) (1 male); Blanchiseusse Road, mile 9, 24 August 1980, D. S. Dobkin (#43) (3 females); same data, (#44), (#45) (numerous specimens); ex *Psiguria tryphylla* (Miq.) C. Jeffrey (Cucurbitaceae), Arima Valley, 50 m S Scott's Quarry, 17 February 1979, R. K. Colwell (#T219) (1 female, 2 males); ex *Costus scaber* Ruiz & Pavón (Zingiberaceae), Blanchiseusse Road, mile 19, 11 March 1979, R. K. Colwell (#T247) (2 females).

Specimens collected from hummingbirds include the following phoretic hosts: ex *Amazilia chionopectus chionopectus* (Gould), Arima Valley, Simla, 15–18 February 1976, R. K. Colwell (#U1, U2) (4 females); ex *Amazilia tobaci erythronotos* (Lesson), Arima Valley, Simla, 21–24 July 1975, R. K. Colwell (#T41, T42, T43) (7 females, 2 males); same locality, 15 February 1976, R. K. Colwell (#U11, U16) (4 females, 3 males); Arima Valley, Lower La Laja Trace, 23–24 February 1976, R. K. Colwell (#U12, U13, U15) (9 females, 2 males); ex *Chlorestes notatus notatus* (C. Reichenbach), Andrews Trace, 2 August 1975, R. K. Colwell (#T17) (1 female); Arima Valley, Simla, 30 July–2 August 1975, R. K. Colwell (#T24, T40) (5 females); Lower La Laja Trace, 24 February 1976, R. K. Colwell (#U9) (2 females); Arima Valley, Simla, 18–20 February 1976, R. K. Colwell (#U4, U5) (2 females); ex *Glaucis hirsuta insularum* Hellmayr and Seilern, La Laja Trace, 11 August 1975, R. K. Colwell (#T44) (1 female); Arima Valley, Simla, 24 July 1975, R. K. Colwell (#T50) (6 females); same locality, 15–20 February 1976, R. K. Colwell (#U22, U23, U25, U27, U29, U34, U38, U43, U44, U45, U46, U47) (64 females, 26 males); ex *Phaethornis guy guy* (Lesson), Andrews Trace, 30 December 1973, R. K. Colwell (#T36) (6 females); Arima Valley, Simla, 18 February 1976, R. K. Colwell (#U17) (1 female).

SPECIMEN DEPOSITION.—Voucher specimens are deposited in the following institutions: UMMZ, NMNH, BYU, CNC.

COMMENTS.—Our specimens agree closely with the descriptions given by Fain et al. (1977b) except that the anterior pair of sternal setae in the female are more widely spaced as in other members of the *kirmsei*-group (26–31 μm vs. 21 μm as given by Fain et al.). Colwell (1986a, 1986b) and Heyneman et al. (1990) have noted the seasonal shift in primary host plants exhibited by this species. The preferred host plant in the wet season is *Hamelia patens*, while *Palicourea crocea* is used preferentially in the dry season. It should be noted that our specimens collected during the wet season averaged slightly larger than specimens taken during the dry season. As the type-series was collected during the dry season, the somewhat larger average measurements given above for the species as a whole are explained by the inclusion of wet-season individuals.

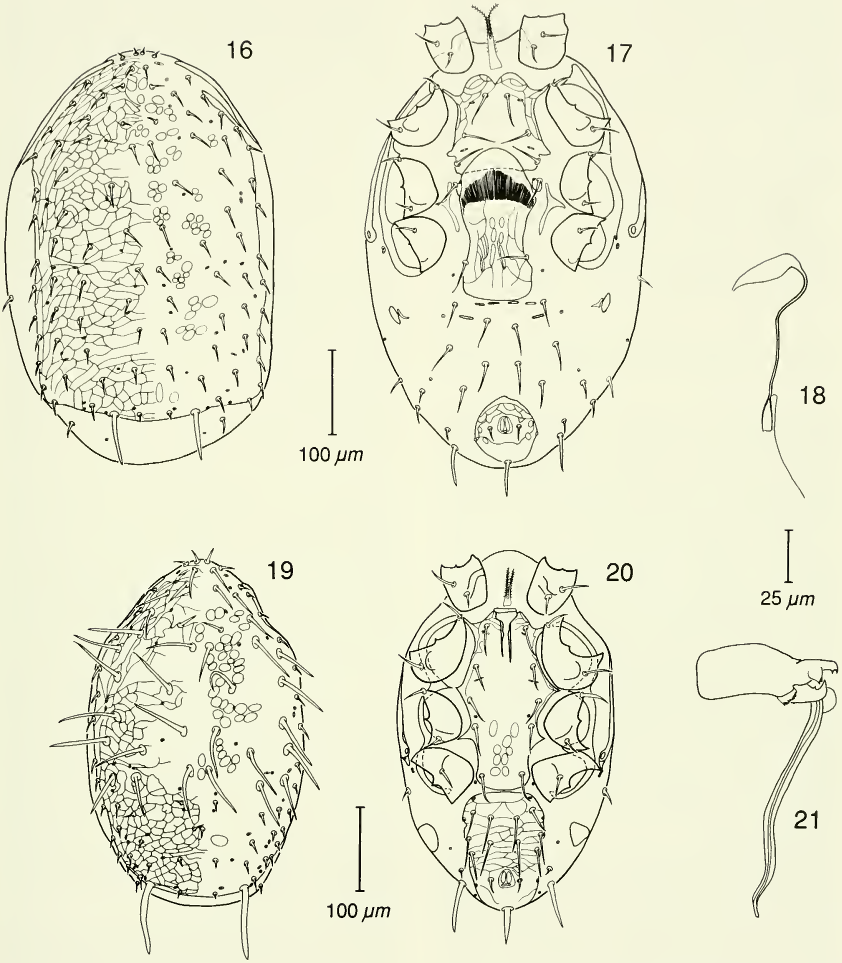
***Proctolaelaps jurgatus*, new species**

Proctolaelaps jurgatus Colwell, 1986: 408, nomen nudum

Proctolaelaps jurgatus Heyneman et al., 1990: 468, nomen nudum

FEMALE (Figs. 16–18).—Idiosomal length 599, 536 (486–631), width 363, 332 (291–383); dorsal shield length 478, 453 (416–485), width 284, 265 (247–285) ($n = 10$). Dorsal shield (Fig. 16) with reticulate pattern over entire surface. Dorsal shield with 44 pairs of smooth, simple setae; marginal setae r2–6 and R1–6 on edge of shield, R7 on membrane posterior to shield, an additional marginal seta (r1) occasionally present unilaterally as on holotype; 3 pairs of submarginal setae (UR) on lateral membrane posteriad of coxae IV. The following measurements of dorsal setae were taken from the holotype, a mite of somewhat larger than average body size: setae j1, j4, and z1 very short (9–11 μm), setae j2–3, z3, s1–2 longer (15–18 μm), other anterior setae longer (22–29 μm); posterior half of shield with anterior median setae J1, Z1, and S1 longer (20–24 μm) than most other setae (15 μm), J5 a microseta (9 μm) and Z5 a stout, elongate spine (64 μm); all marginal setae 15–22 μm long. Glands, proprioceptors, and muscle scars positioned as indicated in Figure 16.

Venter (Fig. 17) with tritosternum with elongate base and slender, tapering, pilose laciniae. Sternal shield longer than wide, with 3 pairs of relatively long setae and 2 pairs of pores, lengths of setae greater than or equal to distance between st2 and st3; anterior lobes and lateral margins of shield with distinct linear pattern. Fourth pair of sternal setae and 3rd pair of sternal pores on metasternal



Figs. 16–21. *Proctolaelaps jurgatus:* 16, female dorsum; 17, female venter; 18, female spermathecal system; 19, male dorsum; 20, male venter; 21, male chelicera.

platelets. Genital shield with linear ornamentation, shield widened behind genital setae. Six small sclerites positioned directly posterior to genital shield. Endopodal apodemes distinct between epigynial shield and coxae III–IV; exopodal sclerites extending from between coxae I–II to behind coxae IV. Two pairs of small, elongate metapodal plates. Anal shield ovoid, longer than wide (length 87, 81 [74–94], width 77, 73 [65–79] μm), ornamentation confined to anterior two-thirds, postanal seta slender, about twice as long as paraanal setae. Posterior ventral region with 8 pairs of setae (JV1–5, Zv1–3), Jv1 and Jv2 typically longer than other anterior setae, Jv5 stout and 53 μm long in holotype;

posterior submarginal setae (UR) also typically visible ventrally (Fig. 17). Peritreme extending anteriad to a point between bases of dorsal setae z1 and s1. Spermathecal system consisting of a broad, membranous pouch just inside external opening, connecting with an adductor canal approximately 65–70 μm long; a small, elongate, bell-shaped maturation pouch lies at juncture of adductor canal and the long, thin spermiduct (Fig. 18).

Gnathosoma with tectum variably shaped as in *P. kirmsei*. Chelicera with fixed digit bidentate; movable digit also bidentate with strong distal hook; a large, membranous process bearing 2 distal teeth present on paraxial face. Deutosterum with 7 transverse rows of denticles; anterior 6 rows connected; no rows widened. Rostral setae simple, slender, with internal posterior rostral setae at least twice as long as external posterior rostral setae; capitular setae slender, simple. Corniculi parallel; internal malae very thin, extending to or slightly beyond tip of corniculi. Palps similar to other *Proctolaelaps* species.

Legs I–IV (excluding pretarsi) 81, 72, 73, and 86% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxae II and III with pronounced convex boss, coxa IV with a weaker boss. Setation of genua of legs I, II, III, and IV, respectively, 13-11-9-9, that of tibia: 13-10-8-10; all leg setae setiform to filiform except the following spinelike setae: ad1, ad3, pd1, pd2 of femur I, pd2 of femur II, ad1 of femur III, ad1 and ad2 of femur IV; setae al1 and v of femur IV are setiform, but elongate, about as long as the segment width.

MALE (Figs. 19–21).—Idiosomal length 420 (391–432), width 271 (252–281) (*n* = 10). Reticulate pattern present laterally on shield and on posterior third; central half of shield with pattern very weak or absent (Fig. 19). Shield with 43–45 pairs of setae, posterior marginal (R) setae varying from 5 to 7 pairs, all on shield; anterior marginal seta r1 occasionally unilaterally present as on figured specimen. One pair of submarginals (UR1) laterad of coxae IV. Anterior dorsal setae of j, z, and s series all spinelike; the following measurements of dorsal setae are taken from the figured specimen: j1-17, j2 and j3-42, j4-26, j5-57, j6-68, z1-11, z2-35, z3-44, z4-64, z5-57, z6-64, s1-15, s2-20, s3-57, s4, s5 and s6 all 66 μm; all anterior marginal setae 15–20 μm long. Posterior dorsal setae J1, Z1, and S1 also long spines, 68, 64, and 55 μm long; terminal seta Z5 is a thickened, blunt spine, 92 μm long; other posterior dorsal and marginal setae very short (10–15 μm). Glands, proprioceptors, and muscle scars as shown in Figure 19.

Venter (Fig. 20) with tritosternum with base distinctly shorter than in female. Sternogenital shield with reticulation confined to anteriolateral corners, smooth medially and posteriorly, with 5 pairs of setae and 3 pairs of pores. Metapodal plates triangular to quadrate, much larger than in female. Ventrianal shield relatively narrow, not extending to metapodal plates, reticulated over entire surface, with 5 pairs of ventral setae on shield, Jv1–3, Zv1–2, in addition to paraanal setae. Three pairs of ventral setae (Jv4, Jv5, and Zv3) on membrane, Zv3 strongly displaced dorsolaterally. Setae Jv1, Jv2, Jv3, and Zv2 relatively long and setiform (40–45 μm), Zv1 setiform and somewhat shorter (29 μm); Jv4 and Zv3 short (10–11 μm), and Jv5 a thick, blunt spine, 60–70 μm long. Paraanal setae approximately half as long as thick, blunt postanal seta (35–45 μm). Peritremes much shorter than in female, extending anteriad to the vicinity of seta s1. Endopodal apodemes fused to sternogenital shield; exopodal sclerites well developed laterad of coxae.

Gnathosoma with tectum simpler than in female, broadly rounded and with few or no teeth. Fixed digit of chelicera with one tooth and a bidentate, membranous process as in female; movable digit unidentate, with long, somewhat sinuous spermatodactyl projecting posterioventrally, 114–125 μm long (Fig. 21). Corniculi shorter and stouter than in female, widely spread basally; other features of gnathosoma as on female.

Legs I–IV (excluding pretarsi) 83, 69, 65, and 92% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxa II with pronounced convex boss, coxa III with a weaker boss, coxa IV without boss. Leg I generally similar to female except some setae of femur distinctly more spinelike. Leg II distinctly thickened, setae ad1, pd2, and all three ventral setae in the form of thick spines; genu and tibia each with seta pv a thick spine; tarsus with setae av1–2, pv1–2, and mv with thickened, bulbous base. Leg III with setation generally similar to female but with tarsal setae av1–2, pv1–2, and mv modified as on leg II. Leg IV strongly modified; femur enlarged, with ventral apophysis bearing partially fused, spurlike ventral seta, dorsal setae thickened and spinelike especially ad1; genu with ventral seta with bulbous base; tibia with ventral setae av and pv likewise modified; tarsus with seta mv with bulbous base, setae av1 and av2 distinctly longer than pv1 and pv2. Pretarsi relatively long.

ETYMOLOGY.—The specific name *jurgatus* is from the Latin meaning "quarrelsome" and is an adjective.

MATERIAL EXAMINED.—All specimens from host plants were collected from the flowers of *Isertia parviflora* Vahl. (Rubiaceae) from the following Trinidad localities (all examined specimens are considered paratypes): Arima Valley, Cricket Pitch near Temple Village, 12 March 1979, R. K. Colwell (#T280) (holotype and 2 other females, 4 males); same data (#T281) (1 female, 2 males, 1 deutonymph); same locality, 23 February 1979, R. K. Colwell (#T242) (1 female); same data (#T240) (2 females); Arima Valley, Temple Village, 11 August 1975, R. K. Colwell (#T74) (3 females); Waller Field, 22 February 1976, R. K. Colwell (#U66) (1 male); Waller Field, near entrance, 21 March 1979, R.K. Colwell (#T622) (10 females, 5 males, 4 deutonymphs); same data (#T620, T621, T622) (a large series of specimens).

Specimens collected from hummingbirds include the following phoretic hosts: ex *Amazilia tobaci erythronotos* (Lesson), Waller Field, 23 June 1976, P. Feinsinger (#W2, W3, W4) (21 females); ex *Chlorestes notatus notatus* (C. Reichenbach), Lower La Laja Trace, 23 February 1976, R. K. Colwell (#U8) (1 female); ex *Chrysolampis mosquitus* (Linne), Waller Field, 23 June 1976, P. Feinsinger (#W5, W6, W7, W8, W9) (48 females, 5 males); ex *Phaethornis longuemareus longuemareus* (Lesson), Waller Field, 23 June 1976, P. Feinsinger (#W10, W11, W12, W13) (2 females, 2 males).

SPECIMEN DEPOSITION.—Holotype and paratypes in UMMZ, additional paratypes in NMNH, BYU, CNC, and IRSNB.

COMMENTS.—This species is most closely related to *P. kirmsei,* sharing with that species the derived character states of a bell-shaped maturation pouch in the female spermathecal system and the enlarged central setae of the male dorsum. With respect to other members of the *kirmsei*-group, this species manifests the ancestral conditions of retaining metasternal platelets in the female, retaining dorsal seta z3 in both sexes, having posterior setae z5 and Jv5 simple (not clubbed) spines, and having all marginal setae (except R7) on the dorsal shield.

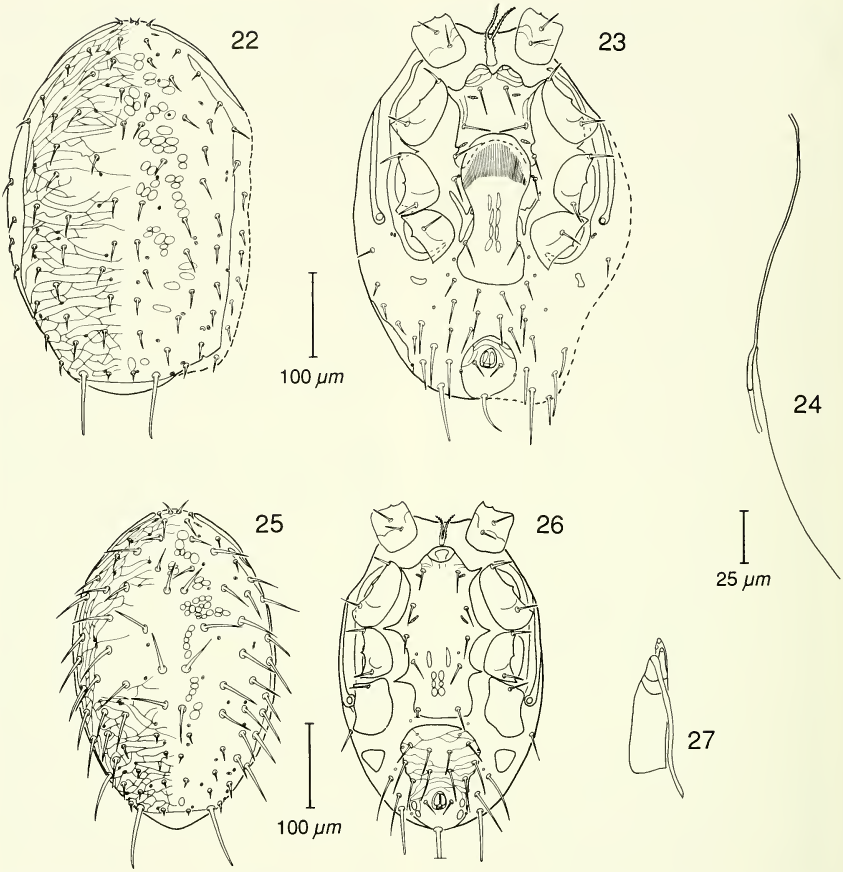
Proctolaelaps jurgatus may be distinguished from *P. kirmsei* in the female by the relatively longer sternal setae, longer maturation pouch in the spermathecal system, and relatively shorter posterior seta Jv5; and in the male by the much greater size of the anterior dorsal setae, especially j1–3, z2–3, and s3.

Proctolaelaps mermillion, new species

Proctolaelaps mermillion Colwell, 1986a: 408, nomen nudum

FEMALE (Figs. 22–24).—The following description is of the holotype and only known female. Idiosomal length 468, width 301 μm; dorsal shield length 456, width 263 μm. Dorsal shield (Fig. 22) with reticulate pattern over entire surface. Dorsal shield with 34 pairs of smooth, simple setae; seta z3 absent; marginal setae r2–3 on shield, other anterior marginals (r4–6) and posterior marginals (R1–7) on membrane lateral to shield (R5 unilaterally absent); 3 pairs of submarginal setae (UR) on lateral membrane posteriad of coxae IV. All setae setiform except Z5, which is an elongate, blunt spine. Setal lengths as follows: j1–6, 7, 11, 13, 15, 18, 22 μm; z1–6 (z3 absent), 7, 20, x, 22, 20, 20 μm; s1–6, 11, 11, 18, 23, 24, 22 μm; posterior half of shield with J1–5, 22, 20, 19, 20, 8 μm; Z1–5, 22, 22, 20, 19, 77 μm; S1–5, 18, 18, 15, 15, 15 μm; all marginal setae 13–15 μm long except R7, which is more spinelike and 33 μm long. Glands, proprioceptors, and muscle scars positioned as indicated in Figure 22.

Venter (Fig. 23) with tritosternum with elongate base and slender, tapering, pilose laciniae. Sternal shield longer than wide, with distinctly concave posterior border, bearing 3 pairs of setae and 2 pairs of pores; anterior lobes of shield well developed, with distinct linear pattern. Fourth pair of sternal setae and 3rd pair of sternal pores on membrane posterior to shield; metasternal platelets absent. Genital shield without linear ornamentation, shield distinctly widened behind genital setae. No small sclerites observed posterior



Figs. 22–27. *Proctolaelaps mermillion:* 22, female dorsum; 23, female venter; 24, female spermathecal system; 25, male dorsum; 26, male venter; 27, male chelicera.

to genital shield. Endopodal apodemes distinct between epigynial shield and coxae III–IV; exopodal sclerites extending from between coxae I–II to behind coxae IV. One pair of small, elongate metapodal plates. Anal shield ovoid, longer than wide, ornamentation confined to anterior half, postanal seta slender, about twice as long as paraanal setae. Posterior ventral region with 8 pairs of setae (JV1–5, Zv1–3) and a supernumerary Zv seta unilaterally; lengths of setae as follows: Jv1–5, 26, 35, 35, 46, 68 μm; Zv1–3, 20, 31, 29 μm; setae setiform to filiform except Jv4–5 and two posterior UR setae, which are thickened spines, the latter being 37 and 48 μm long. Peritreme extending anteriad to a point approximating base of dorsal seta z1. Spermathecal system lacking expanded, membranous pouch inside opening, system consisting of a narrow adductor canal approximately 117 μm long; an elongate maturation pouch 48 μm long, which is divided roughly in half, anterior half more strongly sclerotized; and a thin spermiduct at least 110 μm long (Fig. 24).

Gnathosoma with tectum broadly rounded with few apical teeth. Chelicerae visible only in dorsoventral view, with fixed digit bidentate; movable digit not clearly observed. Deutosterum with 7 transverse rows of denticles; anterior 6 rows connected; no rows widened. Rostral setae simple, slender, with internal posterior rostral setae at least twice as long as external posterior rostral setae; capitular setae slender, simple. Corniculi parallel; internal malae not observed. Palps similar to other *Proctolaelaps* species.

Legs I–IV (excluding pretarsi) 94, 65, 77, and 96% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxae II and III with convex boss, coxa IV with a weaker boss. Setation of genua of legs I, II, III, and IV, respectively, 13-11-9-9, that of tibia: 13-10-8-10; all leg setae setiform to filiform except the following spinelike setae: ad1 of femur III, ad1 and ad2 of femur IV, and v of femur IV, which is strong and about as long as the segment width.

MALE (Figs. 25–27).—The following description is of the single available male specimen. Idiosomal length 386, width 256 µm. Reticulate pattern present on anterior quarter and posterior half and laterally on shield, central region of shield with pattern very weak or absent (Fig. 25). Shield with 41 pairs of setae, z3 absent, only 3 pairs of posterior marginal (R) setae present, all on shield. One pair of submarginals (UR1) laterad of coxae IV. Many dorsal setae elongate and spinelike, lengths of setae: j1–6, 15, 20, 22, 31, 35, 44 µm; z1–6, 9, 42, x, 44, 45, 48 µm; s1–6, 11, 11, 45, 48, 53, 48 µm; posterior setae J1–5, 46, 9, 7, 6, 3 µm; Z1–5, 48, 13, 9, 9, 70 µm; S1–5, 44, 44, 34, 24, 11 µm. All marginal setae elongate and spinelike, lengths of r2–6 and R1–3, 33, 51, 44, 53, 44, 48, 48, 57 µm. Glands, proprioceptors, and muscle scars as shown in Figure 25.

Venter (Fig. 26) with tritosternum with base distinctly shorter than in female. Sternogenital shield with very weak reticulation confined to anteriolateral corners, smooth medially and posteriorly, with 5 pairs of setae and 3 pairs of pores. Metapodal plates triangular, much larger than in female. Ventrianal shield relatively narrow, not extending to metapodal plates, reticulated over entire surface, with 5 pairs of ventral setae on shield, Jv1–3, Zv1–2, in addition to paraanal setae. Three pairs of ventral setae (Jv4, Jv5, and Zv3) on membrane. Setae Jv1–3 and Zv1–3 moderately long and setiform, lengths 33, 40, 41, 24, 42, 53 µm; Jv4 and Jv5 are stouter and spinelike, 53 and 57 µm long. Paraanal setae thin, postanal seta thick, broken in specimen examined. Peritremes similar to female, extending anteriad to the vicinity of seta z1. Endopodal apodemes fused to sternogenital shield; exopodal sclerites well developed laterad of coxae, but difficult to observe due to distortion of legs in specimen.

Gnathosoma with tectum similar to female, broadly rounded and with few teeth. Chelicerae only observed in dorsoventral view; fixed digit of chelicera with one tooth; movable digit not clearly observed, with moderately sized, slightly sinuous spermatodactyl projecting posterioventrally, 73 µm long (Fig. 27). Corniculi shorter and stouter than in female, widely spread basally; other features of gnathosoma as on female.

Legs I–IV (excluding pretarsi) 90, 71, 71, and 97% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxa II with pronounced convex boss, coxa III with a weaker boss, coxa IV without boss. Leg I generally similar to female except some setae of femur slightly more spinelike. Leg II distinctly thickened, setae ad1, pd2, and all three ventral setae in the form of thick spines; genu and tibia each with seta pv a thick spine; tarsus with setae av1–2, pv1–2, and mv with thickened, bulbous base. Leg III with setation generally similar to female but with tarsal setae av1–2, pv1–2 and mv modified as on leg II, although setal bases are not as swollen. Leg IV strongly modified; femur enlarged, with ventral apophysis bearing partially fused, spurlike ventral seta, dorsal setae thickened and spinelike especially ad1; genu with ventral seta with bulbous base; tibia with ventral setae av and pv likewise modified; tarsus with seta mv with bulbous base, setae av1 and av2 distinctly longer than pv1 and pv2. Pretarsi relatively long.

ETYMOLOGY.—The species name *mermillion* is modified from the Greek meaning "gladiator." It is a masculine noun in apposition.

MATERIAL EXAMINED.—Holotype female and 1 paratype male from the nares of *Amazilia chionopectus* (Trochilidae), TRINIDAD: Simla Research Station, 4 mi N Arima, 18 February 1976, R. K. Colwell (#U3).

Two additional female specimens collected from a hummingbird, *Phaethornis guy guy* (Lesson), same locality and date, R. K. Colwell (#U18), were not included in the above description and are not considered paratypes.

SPECIMEN DEPOSITION.—Holotype and paratype in UMMZ.

COMMENTS.—*Proctolaelaps mermillion* is the only species of flower mite we were unable to collect from a host plant in Trinidad. We suspect that the host of this species is an epiphyte because, while our collecting of terrestrial hummingbird-pollinated plants was exhaustive, we were unable to sample some epiphytic species.

This species is most closely related to *P. hunteri*, a species known at present only from Brazil. The two species share the derived character states of loss of dorsal seta z3 in both sexes, posterior marginal setae off the dorsal shield in the female, and the enlargement of the posterior marginal setae in the male. The species differs from *P. hunteri* in the female by the posteriorly concave sternal shield, and by having marginal setae r4–5 off the dorsal shield; male *P. mermillion* lack 4–5 pairs of posterior marginal setae that are present and elongate in *P. hunteri*, and also posterior dorsal setae S3–5 are distinctly shorter in male *P. mermillion*.

Proctolaelaps glaucis **Fain**, Hyland and Aitken, 1977

Proctolaelaps glaucis Fain, Hyland and Aitken, 1977a: 185

Proctolaelaps glaucis Fain, Hyland and Aitken, 1977b: 129

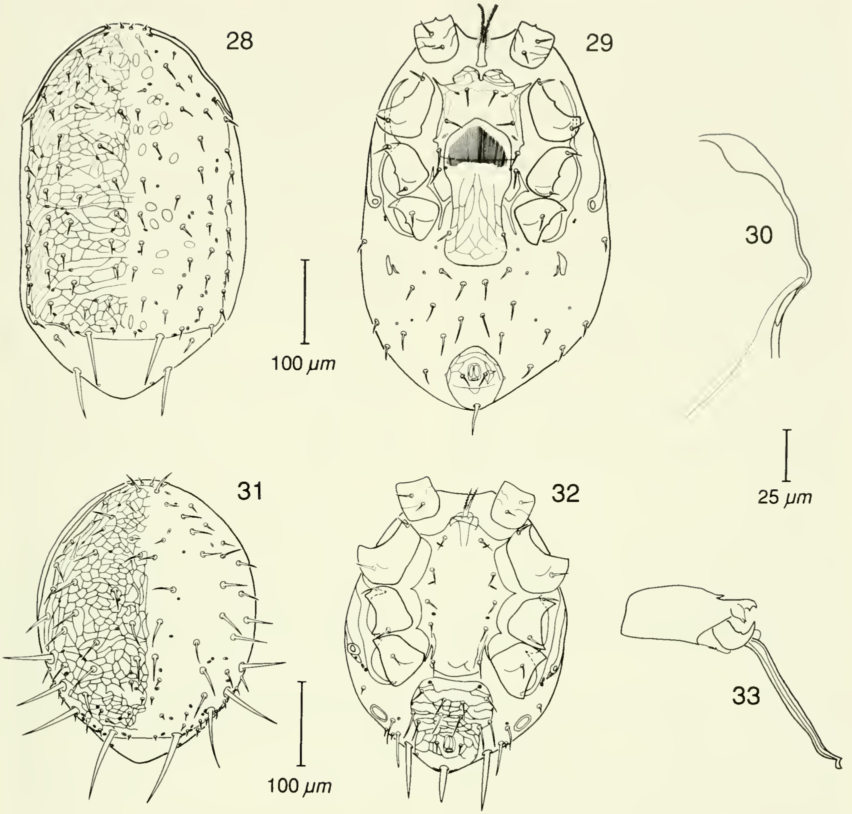
Proctolaelaps glaucis Colwell, 1985: 61

Proctolaelaps glaucis Colwell, 1986a: 408

This species was briefly diagnosed from the holotype female collected from the nares of *Glaucis hirsuta* from "Trinidad" (Fain et al. 1977a). Fain et al. (1977b) provided a more complete description of the female and a brief description of one male; both sexes were figured. All specimens were collected from the nares of *G. hirsuta* from the following Trinidad localities: Ravine Sable Trace–Vega de Oropouche, Esperanza Estate, Corneillac Estate, Fort Read. Some aspects of the ecology and host associations of this species have been discussed by Colwell (1985, 1986a). We give here a redescription of this species based on our collections from Trinidad. Our specimens were compared with the holotype.

FEMALE (Figs. 28–30).—Idiosomal length 462 (439–497), width 318 (281–369) μm; dorsal shield length 400 (386–410), width 258 (246–287) μm ($n = 8$). Dorsal shield (Fig. 28) with reticulate pattern over entire surface. Dorsal shield with 44 pairs of smooth, simple setae; marginal setae r2–6 and R1–6 on edge of shield, R7 on membrane posterior to shield; 3 pairs of submarginal setae (UR) on lateral membrane posteriad of coxae IV. The following measurements of dorsal setae were taken from the figured specimen, a mite of somewhat larger than average body size: j setae very unequal, lengths of j1–6, 8, 22, 18, 9, 18, 20 μm; anterior z setae also unequal, lengths of z1–6, 12, 24, 15, 22, 20, 20, 20 μm; s1–2 both 13 μm, s3–6 all 20–22 μm; posterior dorsal setae (except J5 and Z5) and all marginal setae (r–R) 18–20 μm, J5 very short (7 μm), Z5 long and spinelike (62 μm). Glands, proprioceptors, and muscle scars positioned as indicated in Figure 28.

Venter (Fig. 29) with tritosternum with elongate base and slender, tapering, pilose laciniae. Sternal shield longer than wide, posterior border generally straight, with 3 pairs of setae and 2 pairs of pores; anterior lobes of shield well developed, with distinct linear pattern; linear pattern also present laterally. Fourth pair of sternal setae and 3rd pair of sternal pores on membrane posterior to shield, metasternal platelets absent. Genital shield with linear ornamentation, shield slightly widened behind genital setae. Without small sclerites posterior to genital shield. Endopodal apodemes distinct between epigynial shield and coxae III–IV; exopodal sclerites extending from between coxae I–II to behind coxae IV. Two pairs of metapodal plates, external plate elongate and much larger than internal plate, which was not observed in all specimens. Anal shield wider than long (averaging 70 μm long to 75 μm wide), ornamentation confined to anterior two-thirds, postanal seta spinelike, about twice as long as paraanal setae. Posterior ventral region with 8 pairs of setae (JV1–5, Zv1–3, figured specimen with supernumerary Zv seta unilaterally), Jv1 and Jv2 typically longer than other anterior setae, Jv5 stout and 60–70 μm long; posterior submarginal setae (UR) also typically visible ventrally (Fig. 29). Peritreme extending anteriad to a point approximating base of dorsal seta z1. Spermathecal system (Fig. 30) consisting of a



Figs. 28–33. *Proctolaelaps glaucis:* 28, female dorsum; 29, female venter; 30, female spermathecal system; 31, male dorsum; 32, male venter; 33, male chelicera.

broad, membranous pouch just inside external opening, connecting with an adductor canal approximately 51 μm long; an elongate maturation pouch 42 μm long that is divided roughly in half, anterior half more strongly sclerotized; and a thin spermiduct at least 100 μm long.

Gnathosoma with tectum broadly rounded with few apical teeth. Chelicerae visible only in dorsoventral view, with fixed digit bidentate and bearing a large, membranous process with two distal teeth; movable digit not clearly observed. Deutosterum with 7 transverse rows of denticles; anterior 6 rows connected; no rows widened. Rostral setae simple, slender, with internal posterior rostral setae slightly less than twice as long as external posterior rostral setae; capitular setae slender, simple. Corniculi parallel; internal malae not observed. Palps similar to other *Proctolaelaps* species.

Legs I–IV (excluding pretarsi) 91, 71, 72, and 90% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxae II and III with convex boss, coxa IV with a weaker boss. Setation of genua of legs I, II, III, and IV, respectively, 13-11-9-9, that of tibia: 13-10-8-10; all leg setae setiform to filiform except the following spinelike setae: ad1 of femur III, and ad1 of femur IV; seta v of femur IV longer than other setae but not as long as the segment width.

MALE (Figs. 31–33).—Idiosomal length 347 (316–398), width 257 (222–281) ($n = 10$). Reticulate pattern present covering dorsal shield (Fig. 31). Shield with 43–44 pairs of setae, posterior marginal (R) setae varying from 5 to 7 pairs, all on shield except R7. One pair of submarginals (UR1) laterad of coxae IV. Most anterior and central dorsal setae somewhat elongate and spineline; posterior setae mostly very short except lateral setae S2–3 and r6 and terminal seta Z5, which are very large spines. Dorsal setae exhibiting more length variation than in other species; the following measurements are from the smallest and largest measured males: j1, 7-9; j2, 20-26; j3, 18-18; j4, 11-15; j5, 24-24; j6, 29-37; z1, 7-9; z2, 24-29; z3, 15-20; z4, 26-31; z5, 29-33; z6, 29-31; s1, 10-15; s2, 11-11; s3, 24-30; s4, 30-33; s5, 31-35; s6, 26-35; r2, 13-15; r3, 22-24; r4, 20-24; r5, 24-26; r6, 35-55; posterior setae: J1, 29-37; J2, 7-11; J3, 6-9; J4, 9-9; J5, 4-5; Z1, 29-37; Z2, 29-33; Z3, 13-11; Z4, 11-11; Z5, 70-92; S1, 26-26; S2, 57-66; S3, 57-75; S4, 10-15; S5, 10-10. Posterior marginal setae all approximately 5–9 μm, except R1, which may be somewhat longer when present. Glands, proprioceptors and muscle scars as shown in Figure 31.

Venter (Fig. 32) with tritosternum base distinctly shorter than in female. Sternogenital shield with slight linear ornamentation confined to posteriolateral corners, smooth anteriorly and medially, with 5 pairs of setae and 3 pairs of pores. Metapodal plates difficult to observe, generally hidden by enlarged femora IV; plates ovoid to quadrate, with possibly thickened margins. Ventrianal shield relatively narrow, not extending to metapodal plates, reticulated over entire surface, with 5 pairs of ventral setae on shield, Jv1–3, Zv1–2, in addition to paraanal setae. Three pairs of ventral setae (Jv4, Jv5, and Zv3) on membrane. Setae Jv2, Jv3, and Zv2 setiform and of moderate length (30–33 μm); Jv1, Zv1 setiform and somewhat shorter (20 μm); Jv4 somewhat thicker and 37 μm long; Jv5 a thick, blunt spine, 50–55 μm long. Paraanal setae approximately one-third as long as very thick, blunt postanal seta (38–44 μm). Peritremes much shorter than in female, extending anteriad to the vicinity of seta s1. Endopodal apodemes fused to sternogenital shield; exopodal sclerites well developed laterad of coxae.

Gnathosoma with tectum simpler than in female, broadly rounded and with few or no teeth. Fixed digit of chelicera with one tooth and a bidentate, membranous process as in female; movable digit with a rudimentary tooth, with long, somewhat sinuous spermatodactyl projecting posterioventrally, 88 μm long (no variation); spermatodactyl with a small, apical quadrate process projecting from tip (Fig. 33). Corniculi shorter and stouter than in female, widely spread basally; other features of gnathosoma as on female.

Legs I–IV (excluding pretarsi) 98, 82, 77, and 105% of dorsal shield length. Coxa I with fine linear ornamentation medially and laterally; coxa II with pronounced convex boss, coxae III–IV with a weaker boss. Leg I generally similar to female except some setae of femur slightly more spinelike. Leg II distinctly thickened, setae ad1, pd2, and all three ventral setae in the form of thick spines; genu and tibia each with seta pv a thick spine; tarsus with setae av1–2, pv1–2, and mv with thickened, bulbous base. Leg III with setation generally similar to female but with tarsal setae av1–2 and pv1–2 modified as on leg II. Leg IV strongly modified; femur enlarged, with ventral apophysis bearing partially fused, spurlike ventral seta, dorsal setae thickened and spinelike, especially ad1; genu with ventral seta with bulbous base; tibia with ventral setae av and pv likewise modified; tarsus with seta mv with bulbous base, setae av1 and av2 somewhat longer than pv1 and pv2. Pretarsi relatively short.

MATERIAL EXAMINED.—All specimens from host plants were collected from the flowers of *Centropogon cornutus* (L.) Druce (Lobeliaceae) from the following Trinidad localities: Andrews Trace, 10 mi N Arima, 24 February 1979, R. K. Colwell (#T232) (3 females); same locality, 21 February 1976, R. K. Colwell (#U57) (1 female, 1 male); Blanchicheusse Road, mile 18, 21 February 1976, R. K. Colwell (#U56) (1 female); Blanchicheusse Road, Bridge C2/7, 22 August 1980, D. S. Dobkin (#6, 7, 8) (numerous specimens); Arima Valley, Temple Village, 11 August 1975, R. K. Colwell (#T69) (2 females); Carapo Road, 220 meters E Musica Road, 22 February 1979, R. K. Colwell and D. S. Dobkin (#T234) (5 males); Heights of Guanapo Road, 29 December 1973, R. K. Colwell (#T62) (2 females).

Specimens collected from hummingbirds include the following phoretic hosts: ex *Amazilia chionopectus chionopectus* (Gould), La Laja Trace, 10 August 1975, R. K. Colwell (#T30) (1 female); ex *Glaucis hirsuta insularum* Hellmayr and Seilern, Arima Valley, Simla, 22–30 July 1975, R. K. Colwell (#T21, T46, T49, T50, T51, T52, T53) (27 females); same locality, 18 February 1976, R. K. Colwell (#U22, U34) (10 females, 1 male); Andrews Trace, 30 December 1973, R. K. Colwell (#T29) (7 females); Laja Trace, 8–10 August 1975, R. K. Colwell (#T31, T32, T45) (11 females, 2 males).

SPECIMEN DEPOSITION.—Figured voucher specimens deposited in UMMZ, other specimens in NMNH, BYU, CNC, IRSNB.

COMMENTS.—Our specimens agree well with the species as redescribed by Fain et al. (1977b). However, our interpretation of the posterior lateral chaetotaxy of the male dorsum differs from that presented by the previous authors who had only a single male available for examination. We regard the setae identified by Fain et al. (1977b, Fig. 88) as S1, S2, S3, and S4 as actually r6, S1, S2, and S3, respectively. As the lengths of these setae were used as diagnostic characters in their key ("Setae S3 and S4 much heavier and longer . . . than S2 and S1" [p. 121]), it should be noted that setae S4 are actually very short and S2 are long.

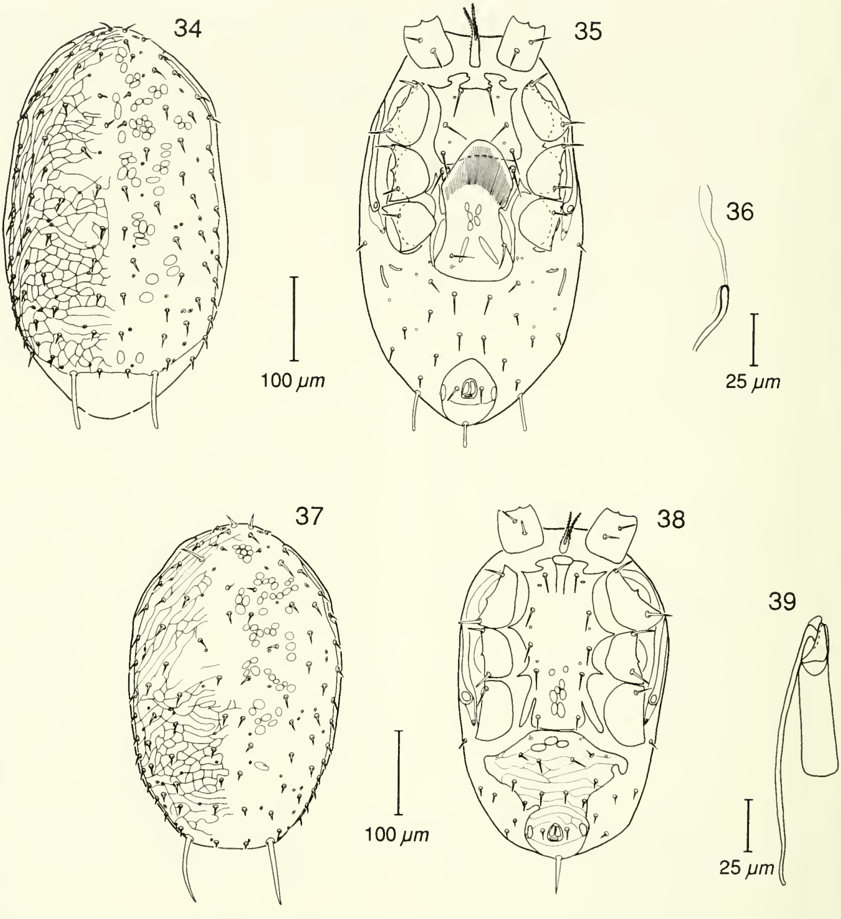
Within the *kirmsei*-group, *P. glaucis* shares the loss of the female metasternal platelets and enlargement of male setae r6, S2, and S3 with *P. hunteri* and *P. mermillion*, conditions we regard as derived. The species retains dorsal setae z3 in both sexes, most marginal setae on the dorsal shield in the female, and relatively short posterior marginal setae in the male, ancestral states which are modified in *P. hunteri* and *P. mermillion*. *P. glaucis* also differs in retaining a completely ornamented male dorsum, an ancestral state in the genus.

Proctolaelaps rabulatus, new species

Proctolaelaps rabulatus Colwell, 1986a: 408, nomen nudum

FEMALE (Figs. 34–36).—Idiosomal length 486, 480 (456–527), width 287, 301 (257–333) μm; dorsal shield length 427, 434 (410–456), width 281, 266 (246–287) μm (*n* = 10). Dorsal shield (Fig. 34) with reticulate pattern over entire surface, more weakly developed anteromedially. Dorsal shield with 43 pairs of smooth, simple setae; anterior seta z3 absent; marginal setae r2–6 and R1–6 on edge of shield, R7 on membrane posterior to shield; only 2 pairs of submarginal setae (UR) on lateral membrane posteriad of coxae IV. Dorsal setae relatively short and setiform, lengths very uniform between 14–17 μm except as follows: z1, s1–2, and J5 shorter, 7–9 μm; j2 and z2 slightly longer, 20–22 μm; Z5 a large spine, 75 μm, seta appearing slightly clubbed in some specimens. Seta j2 unilaterally absent on holotype. Glands, proprioceptors, and muscle scars positioned as indicated in Figure 28.

Venter (Fig. 35) with tritosternum with elongate base and slender, tapering, pilose laciniae. Sternal shield about as long as wide, anterior border deeply incised medially to level of anterior sternal setae; posterior border slightly concave; shield with 3 pairs of setae and 2 pairs of pores; shield smooth, without linear ornamentation. Fourth pair of sternal setae and 3rd pair of sternal pores on metasternal platelets. Genital shield smooth, without linear ornamentation; genital setae on edges of shield (unilaterally anomalous in holotype, with both genital and paragenital seta well on shield); shield distinctly widened behind genital setae. One pair of very short paragenital setae present lateral to genital shield posterior to level of genital setae. Without small sclerites posterior to genital shield. Endopodal apodemes distinct between epigynial shield and coxae III–IV; exopodal sclerites extending from between coxae I–II to behind coxae IV. Two pairs of metapodal plates, external plate very long and thin and much larger than transverse internal plate. Anal shield distinctly longer than wide, ornamentation very weak behind anus, postanal seta spinelike, appearing slightly clubbed in some specimens, about twice as long as paraanal setae. Posterior ventral region with 8 pairs of short setae (JV1–5, Zv1–3), Jv1 and Jv2 typically longer than other anterior setae, Jv5 stout and slightly clubbed in some specimens, 48 μm long; posterior submarginal setae (UR) also typically visible ventrally (Fig. 35). Peritreme extending anteriad to a point approximating base of dorsal seta s1. Spermathecal system (Fig. 36)



Figs. 34–39. *Proctolaelaps rabulatus:* 34, female dorsum; 35, female venter; 36, female spermathecal system; 37, male dorsum; 38, male venter; 39, male chelicera.

consisting of a very membranous adductor canal approximately 100 μm long; an elongate maturation pouch 33 μm long, which is undivided; and a short, thin spermiduct, which is difficult to observe.

Gnathosoma with tectum steeply triangular, without teeth. Chelicerae visible only in dorsoventral view, with fixed digit bidentate and bearing a large, membranous process with two distal teeth; movable digit with at least one tooth. Deutosterum with 7 transverse rows of denticles; rows of denticles wider than in other species and not connected by longitudinal grooves laterally. Rostral setae simple, slender, with internal posterior rostral setae slightly less than twice as long as external posterior rostral setae; capitular setae slender, simple. Corniculi parallel; internal malae not observed. Palps similar to other *Proctolaelaps* species.

Legs I–IV (excluding pretarsi) 85, 71, 70, and 93% of dorsal shield length. Coxae without linear ornamentation or convex bosses. Setation of genua of legs I, II, III, and IV, respectively, 13-11-9-9, that of tibia: 13-10-8-10 (al2 absent unilaterally from genu III in holotype); all leg setae setiform to filiform except the following spinelike setae: ad1 and pd2 of femur I, ad1 and pd2 of femur II, ad1 of femur III, ad1 and ad2 of femur IV; seta v of femur IV not enlarged.

MALE (Figs. 37–39).—Idiosomal length 410 (392–433), width 253 (240–275) (*n* = 4). Reticulate pattern present covering dorsal shield except in median area on anterior half of shield (Fig. 37). Shield with 43 pairs of setae (z3 absent); most marginal setae normally on shield except R7 on membrane posterioventral to shield. Two pairs of submarginals (UR1) laterad of coxae IV. Dorsal setation essentially similar to female, without enlarged setae (except z2 distinctly longer than others as in female, and spinelike Z5). Glands, proprioceptors, and muscle scars as shown in Figure 37.

Venter (Fig. 38) with tritosternum base distinctly shorter than in female. Sternogenital shield without linear ornamentation, with 5 pairs of setae and 3 pairs of pores. Ventrianal shield widened anteriorly, incorporating metapodal plates, reticulated over entire surface, with 5 pairs of ventral setae on shield, Jv1–3, Zv1–2, in addition to paraanal setae; very short paragenital setae present on anterior edge of shield. Three pairs of ventral setae (Jv4, Jv5, and Zv3) on membrane. All ventral setae short and setiform (including Jv5), Jv1 longest (15 μm), others 7–10 μm. Paraanal setae approximately one-third as long as very thick, blunt postanal seta (44 μm). Peritremes similar to female, extending anteriad to the vicinity of seta s1. Endopodal apodemes fused to sternogenital shield; exopodal sclerites well developed laterad of coxae.

Gnathosoma with tectum triangular as in female, without teeth. Chelicerae visible only in dorsoventral view, dentition not observable; with long, straight spermatodactyl projecting posterioventrally, 130 μm long (Fig. 39). Corniculi shorter and stouter than in female, widely spread basally; other features of gnathosoma as on female.

Legs I–IV (excluding pretarsi) 84, 70, 70, and 93% of dorsal shield length. Coxae without linear ornamentation or convex bosses. Leg I generally similar to female except some setae of femur slightly more spinelike. Leg II distinctly thickened, setae ad1, pd2, and all three ventral setae in the form of thick spines; genu and tibia each with seta pv a thick spine; tarsus with setae av1–2, pv1–2, and mv with thickened, bulbous base, although less modified than in other members of the *kirmsei*-group. Leg III with setation generally similar to female but with tarsal setae av1–2, and pv1–2 modified as on leg II. Leg IV strongly modified; femur enlarged, with ventral apophysis bearing partially fused, spurlike ventral seta, seta uniquely modified, having a very obvious tooth about midway along seta; dorsal femoral setae thickened and spinelike, especially ad1; genu with ventral seta with bulbous base; tibia with ventral setae av and pv likewise modified; tarsal setae generally unmodified. Pretarsi relatively short.

ETYMOLOGY.—The specific name *rabulatus* is from the Latin meaning "brawling."

MATERIAL EXAMINED.—All specimens were collected from the flowers of *Mandevilla hirsuta* (A. Rich.) K. Schum. (Apocynaceae) from the following Trinidad localities: Arima Valley, Temple Village, Cricket Pitch, 17 February 1979, R. K. Colwell (#T225) (holotype and 1 paratype female, 2 paratype males); Waller Field, 25 August 1980, D. S. Dobkin (#65) (5 females, 2 males); same data (#66) (3 females). No specimens are yet known from hummingbird phoretic hosts.

SPECIMEN DEPOSITION.—Holotype female and figured paratype male deposited in UMMZ, other paratypes in NMNH, BYU, CNC.

COMMENTS.—This species shares certain characteristics with *P. mexicanus*, notably the widened deutosternal denticle rows, and the tendency for the large, posterior setae to become clubbed. This latter condition is much more obvious in immatures of *P. rabulatus* than in the adults. These species retain certain ancestral character states suggesting that they may be the sister-group of a clade containing the remaining species in the group. These include the lack of modification of the male dorsal setation and the widened ventrianal shield of the male (more so in *P. rabulatus* than in *P. mexicanus*). *P. rabulatus* may be readily distinguished from *P. mexicanus* by possession of derived states including: in both sexes presence of paragenital setae and absence of dorsal seta z3, and in the male by the short form of seta Jv5 and the toothed ventral seta of femur IV. *P. rabulatus* retains the ancestral states of most marginal setae on the dorsal shield and metasternal platelets present in the female.

The *Proctolaelaps belemensis* group.

We group the remaining New World flower-inhabiting *Proctolaelaps* as the "*belemensis*-group." Fain et al. (1977a, 1977b) described *P. belemensis* from numerous species of hummingbirds from Brazil, Panama, Venezuela, and Trinidad. They noted that this species "differs markedly" (p. 133) from the other flower-associated *Proctolaelaps* and listed a set of character states that we regard as a combination of ancestral and derived conditions. Two additional taxa, *P. cyanocompsae* (new status) and *P. spiralis*, share the derived character states that diagnose this group. These species share the hypothetically apomorphic character states of enlargement of dorsal setae j1 in both sexes and the strongly tapered epigynial plate in the female. These species are otherwise rather more plesiomorphic than species in the *kirmsei*-group. Both sexes retain expanded posterior rows of deutosternal teeth and more strongly developed ornamentation on the ventral sclerites. Also males have a broad ventrianal sclerite and simple setae on the legs, and the enlarged seta v of femur IV retains a movable articulation and is not borne on a cuticular tubercle.

During our initial work in Trinidad, we identified mites exhibiting these characteristics from many host plants as *P. belemensis* (e.g., Colwell 1979). Closer examination of morphology, behavior, and host associations allowed us to distinguish four distinct forms that differ primarily in body size, lengths of posterior and marginal setae, and male spermatodactyl morphology. Because these forms exhibit distinct host plant preferences, and no morphological intermediates were discovered, we regard them as separate species. Similarly, because two of these new species are more similar to the previously named "subspecies" *cyanocompsae* than to the nominate subspecies, we give full specific status to the former. Because the morphological differences among these species are relatively minor compared with species in the *kirmsei*-group, a cautionary note is in order. Downes (1990) demonstrated that development in different freshwater mussel hosts can significantly affect the morphology of unionicolid water mites to the extent that offspring of a single female raised on different hosts can exhibit adult morphologies of more than one previously recognized "species." Such host effects could certainly account for character differences such as body size exhibited by the *belemensis*-group species described below. On the other hand, these species are also easily distinguished by male spermatodactyl morphology, a genitalic character that is perhaps less prone to influence by host plant morphology (Eberhard 1985). Experimental transfers of juvenile flower mites to other host plants or study of characters not influenced by host plant morphology or chemistry such as allozymes or nucleic acid sequences will provide the test for the hypothesis that our collections represent distinct species.

The four species of the *belemensis*-group collected in Trinidad are very similar. So, in order to conserve space, a full description is given only for *P. belemensis*. The new species are diagnosed with reference to that species, *P. cyanocompsae*, and each other.

Specimens referrable to the *belemensis*-group were collected in the Arima Valley and at Waller Field, Trinidad, from 4 species of hummingbirds (1973–1976): *Chlorestes notatus notatus* (C. Reichenbach) (1 female on 1 bird), *Glaucis hirsuta insularum* Hellmayr and Seilern (60 females and 9 males on 25 birds), *Phaethornis guy guy* (Lesson) (13 females and 1 male on 5 birds), *Phaethornis longuemareus longuemareus* (Lesson) (5 females on 2 birds). These specimens will not be listed separately after the species accounts because they had not yet been identified to the species level at the time of this writing.

Proctolaelaps belemensis **Fain, Hyland and Aitken, 1977**
Proctolaelaps belemensis Fain, Hyland and Aitken, 1977a: 185
Proctolaelaps belemensis Fain, Hyland and Aitken, 1977b: 133
Proctolaelaps belemensis Hyland, Fain and Moorhouse, 1978: 263
Proctolaelaps belemensis Colwell, 1986a: 408
NOT *Proctolaelaps belemensis* Colwell, 1979: 463

This species was briefly diagnosed from female and male specimens collected from the nares of *Threnetes leucurus* from Belem, Brazil (Fain et al. 1977a). A more complete description, figures of both sexes, and new host and locality records were given later

(Fain et al. 1977b). The latter authors listed *Campylopterus largipennis*, *Phaethornis superciliosus*, and *Glaucis hirsuta* as additional hummingbird hosts and recorded the species from additional localities in Brazil, Panama, Venezuela, and two localities in Trinidad: Cumuto and Ravine Sable Trace, Vega de Oropouche. Hyland et al. (1978) recorded the species from Mexico from *P. superciliosus* and *Campylopterus hemileucurus*. In the published descriptions, measurements were given only for the holotype female and one male specimen. Because only a single male and female attributable to this species were collected during our studies, we include in the following redescription some data taken from two female paratypes and one female from the Mexican collection reported by Hyland et al. (1978).

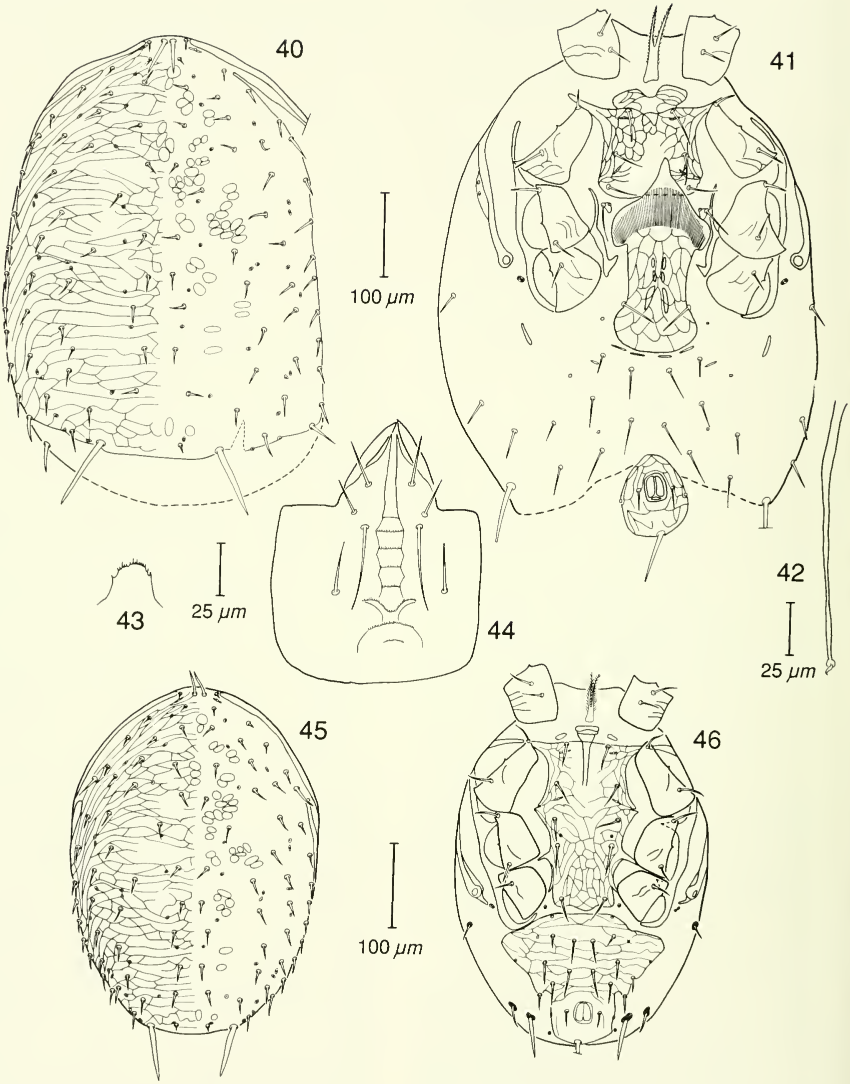
FEMALE (Figs. 40–44).—Idiosomal length of Trinidad specimen 591, in other specimens examined length range (573–620) μm, width 468 (421–439); dorsal shield length 521 (538–565), width 380 (392–404) μm. Dorsal shield (Fig. 40) with transverse, linear pattern over entire surface, reticulations largely confined to posterior edge and median area. Dorsal shield with 44 pairs of smooth, simple setae; marginal setae r2–6 and R1–6 on edge of shield, R7 on membrane posterior to shield; 3 pairs of submarginal setae (UR) on lateral membrane posteriad of coxae IV. The following measurements of dorsal setae were taken from the figured Trinidadian specimen: j1 a stout spine, 44 μm long; j2, z1, s1, and J5 shorter than other dorsal setae, about 13–15 μm (J5 unilaterally absent); most other dorsal setae subequal, 20–24 μm, Z5 a stout spine, 88 μm; most marginal setae similar in length to dorsal setae, r3 and R7 longer than others, both 33 μm. Glands, proprioceptors, and muscle scars positioned as indicated in Figure 40.

Venter (Fig. 41) with tritosternum with elongate base and slender, tapering, pilose laciniae. Sternal shield longer than wide, posterior border generally straight, with 3 pairs of setae and 2 pairs of pores; anterior lobes of shield very weakly sclerotized, but with distinct linear pattern; reticulate pattern also present over most of shield except central and posterior areas. Fourth pair of sternal setae and 3rd pair of sternal pores on metasternal platelets. Genital shield with reticulate ornamentation, shield distinctly widened behind genital setae. With 6 small transverse sclerites posterior to genital shield. Endopodal apodemes distinct between epigynial shield and coxae III–IV; exopodal sclerites extending from middle of coxae II to behind coxae IV. One pair of elongate metapodal plates. Anal shield longer than wide, reticulate ornamentation covering most of shield; postanal seta spinelike, at least twice as long as paraanal setae. Posterior ventral region with 7 pairs of filiform setae (JV1–4, Zv1–3), Jv5 a stout spine; lengths of Jv1–5, 40, 46, 44, 37, 75 μm, Zv1–3, 22, 44, 26 μm. Posterior submarginal setae (UR) also typically visible ventrally (Fig. 41). Peritreme extending anteriad to a point approximating base of dorsal seta z1. Spermatheccal system (Fig. 42) simple, consisting of an adductor canal wider nearer to external opening, approximately 132 μm long; a very short, bulbous maturation pouch at inner terminus of canal; and a very short, hooked spermiduct.

Gnathosoma with tectum rounded and strongly toothed (Fig. 43). Chelicerae visible only in dorsoventral view, with fixed digit bearing a row of small teeth along the length of the dight and a large, membranous antiaxial process with two distal teeth; movable digit not clearly observed. Subcapitulum (Fig. 44) with deutosterum having 7 rows of denticles; anterior 6 rows connected; 5th and 6th rows widened. Rostral setae simple, slender, with internal posterior rostral setae more than twice as long as external posterior rostral setae; capitular setae slender, simple. Corniculi convergent; internal malae not observed. Palps similar to other *Proctolaelaps* species.

Legs I–IV (excluding pretarsi) 110, 87, 76, and 109% of dorsal shield length. All coxae with transverse lines ventrally, without bosses. Setation of genua of legs I, II, III, and IV, respectively, 13-11-9-9, that of tibia: 13-10-8-10; all leg setae setiform to filiform, tarsal setae especially long; without spinelike setae.

MALE (Figs. 45–46).—Redescription based on single Trinidadian male. Idiosomal length 430 μm, width 316 μm Reticulate pattern present covering dorsal shield (Fig. 45). Shield with 44 pairs of setae, all marginal setae on shield except R7. One pair of submarginals (UR1) laterad of coxae IV. Relative lengths of dorsal setae as in female; j1-33, r3-29, R7-26,


40
41
100 µm
42
43
25 µm
44
25 µm
45
46
100 µm

Figs. 40–46. *Proctolaelaps belemensis:* 40, female dorsum; 41, female venter; 42, female spermathecal system; 43, female tectum; 44, female subcapitulum; 45, male dorsum; 46, male venter.

Z5-62 μm; most other dorsal setae 11–15 μm. Glands, proprioceptors and muscle scars as shown in Figure 45.

Venter (Fig. 46) with tritosternum shorter than in female. A pair of small, pre-endopodal sclerites adjacent to genital opening. Sternogenital shield with reticulate pattern well developed over entire shield except anteriomedially, with 5 pairs of setae and 3 pairs of pores. Ventrianal shield widened anteriorly, incorporating metapodal plates, reticulated over entire surface, with 7 pairs of ventral setae on shield, Jv1–4, Zv1–3, in addition to paraanal setae; thickened seta Jv5 on membrane; other setae filiform, relative lengths as in female. The unilateral absence of Zv3 and the position of Jv4 on small extensions of the ventrianal plate are interpreted here as anomalies. Jv4 is off the plate in the "allotype" described for this species, as well as in all other species of the *belemensis*-group. Paraanal setae relatively short, blunt postanal seta broken. Peritremes as in female, extending anteriad to the vicinity of seta z1. Endopodal apodemes fused to sternogenital shield; exopodal sclerites well developed laterad of coxae.

Gnathosoma with tectum as in female, broadly triangular and toothed. Chelicerae only visible in dorsoventral view. Cheliceral digits similar to female; spermatodactyl essentially straight, projecting posterioventrally, 140 μm long; other features of gnathosoma as on female.

Legs I–IV (excluding pretarsi) 118, 88, 79, and 114% of dorsal shield length. Coxae with linear ornamentation as in female. Legs generally similar to female except some setae shorter and more spinelike; these include av1 of femur I, av1 of femur II, av and pv of genu II, and pv of genu III. Ventral seta of femur IV enlarged, but with movable articulation. Pretarsi all elongate.

MATERIAL EXAMINED.—In addition to two paratypes from the type locality in Brazil kindly provided by Dr. Fain, we have examined one of the Mexican specimens reported by Hyland et al. (1978) and the following specimens from Trinidad: from flowers of *Monotagma spicatum* (Aubl.) Macbr. (Marantaceae), La Laja Trace, 8 mi N Arima, 17 February 1976, R. K. Colwell (#U64) (figured female and male).

SPECIMEN DEPOSITION.—Figured voucher specimens deposited in UMMZ.

COMMENTS.—Our specimens generally agree with the published description and figures. The presence of setae Jv4 on the ventrianal shield of the male is regarded as an anomaly in our specimen. This species is one of two relatively small species in the group. Differences between this species and the other small species, *P. contumex*, are discussed below.

We believe it is unlikely that *Monotagma spicatum* is the true host plant of *P. belemensis* for two reasons. First, although more than a hundred flowers of this plant were examined, only two specimens of *P. belemensis* were found. Second, the phoretic hosts from which *P. belemensis* has been collected elsewhere (*Glaucis hirsuta*, *Threnetes leucurus*, *Phaethornis superciliosus*, *Campylopterus largipennis*, and *C. hemileucurus* [Fain et al. 1977a, 1977b, Hyland et al. 1978]) all have long bills (3.2, 3.2, 3.8, 3.8, and 3.3 cm, respectively), whereas the flowers of *Monotagma spicatum* are less than 2 cm in length. In general, hummingbirds feed on flowers that approximate their bill length (Feinsinger and Colwell 1978). The true host plant (or plants) of *P. belemensis* thus, almost surely, has flowers more than 3 cm in length.

Proctolaelaps contumex, new species

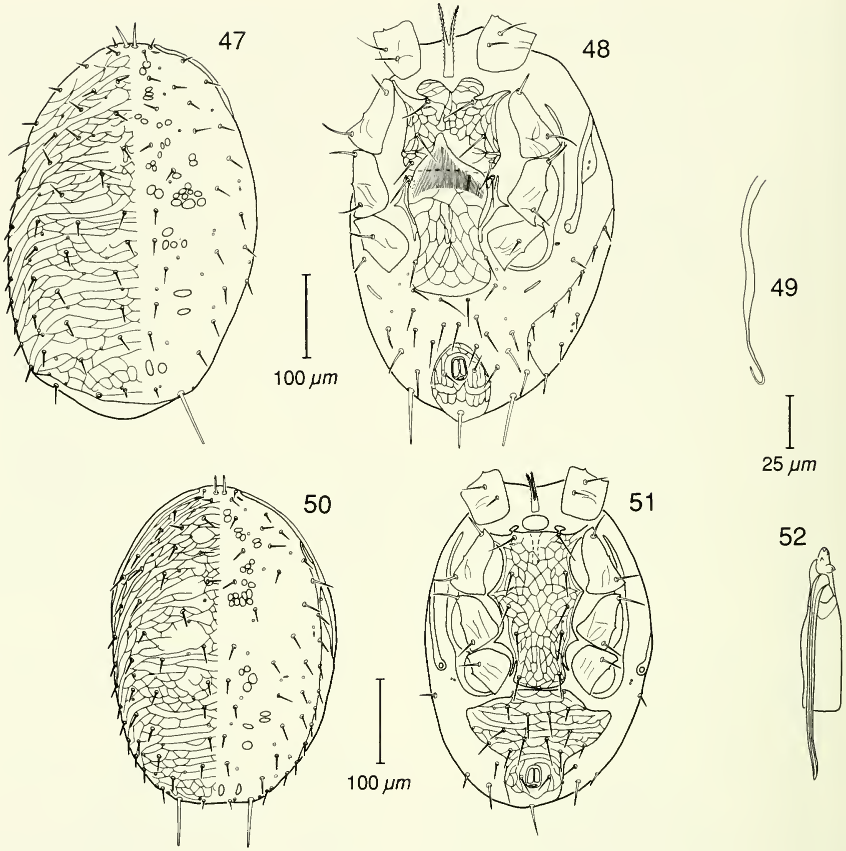
Proctolaelaps belemensis Colwell, 1979: 463, NOT *P. belemensis* Fain, Hyland and Aitken, 1977

Proctolaelaps contumex Colwell, 1986a: 408, nomen nudum

DIAGNOSIS.—This species is very similar to *P. belemensis*. Females (Figs. 47–49) differ primarily in the distinctly smaller body size (idiosomal length of holotype and paratype, 468–538 μm, width 328–363 μm; dorsal shield length 450–456, width 322–328 μm), and the form of the spermathecal system, which consists of a long, simple tube that is thickened towards the exterior and tapers to a fine point, entire tube 123 μm long (Fig. 49). Body setae proportioned as in *P. belemensis*, but setae absolutely shorter.

MALE (Figs. 50–52)—Similar to *P. belemensis* but smaller, both specimens with idiosomal length 410 μm, width 254–281 μm. Spermatodactyl (Fig. 52) much shorter than in *P. belemensis*, length 100–105 μm. Most body setae proportioned as in *P. belemensis*, but setae absolutely shorter; posterior ventral seta Jv5 only slightly enlarged, 33 μm long.

ETYMOLOGY.—The specific name *contumex* is modified from the Latin *contumax*, meaning "defiant" and is an adjective.



Figs. 47–52. *Proctolaelaps contumex:* 47, female dorsum; 48, female venter; 49, female spermathecal system; 50, male dorsum; 51, male venter; 52, male chelicera.

MATERIAL EXAMINED.—All specimens were collected from flowers of *Cephaelis muscosa* Sw. (Rubiaceae) as follows: Blanchiseusse Road, mile 19, 13 March 1979, R. K. Colwell (#T275) (holotype and one other female, 1 male, 1 larva); Arima Valley, Temple Village, Cricket Pitch, 16 February 1979, R. K. Colwell (#T201) (1 male).

SPECIMEN DEPOSITION.—Holotype female and 1 paratype male in UMMZ, other paratypes in BYU.

***Proctolaelaps certator*, new species**

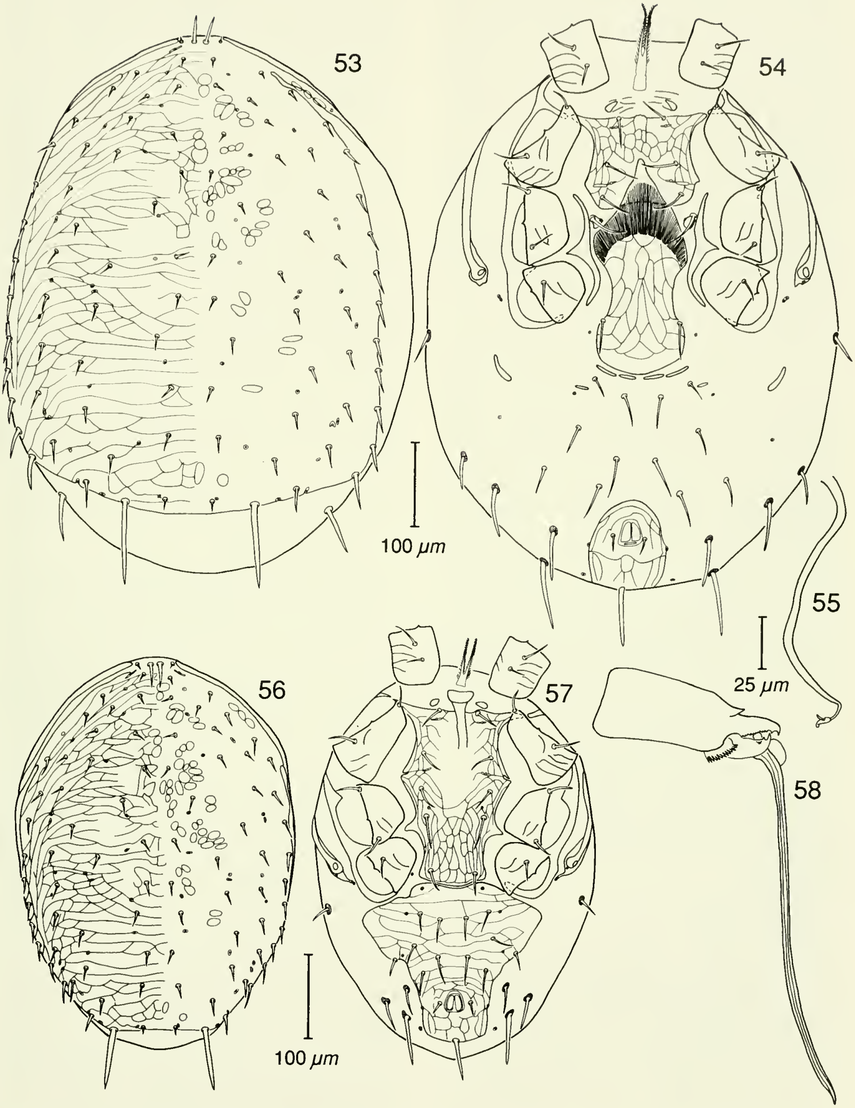
Proctolaelaps certator Dobkin, 1985: 536, nomen nudum

Proctolaelaps certator Colwell, 1986a: 408, nomen nudum

Proctolaelaps certator Colwell, 1986b: 491, nomen nudum

Proctolaelaps certator Heyneman et al., 1990: 468, nomen nudum

FEMALE (Figs. 53–55).—Idiosomal length 620, 659 (556–702), width 468, 496 (445–527) μm; dorsal shield length 573, 562 (544–585), width 450, 430 (404–450) μm ($n = 10$). Dorsal shield (Fig. 53) with transverse, linear pattern over entire surface, reticulations largely confined to median area. Dorsal shield with 44 pairs of smooth, simple setae; marginal


53
54
55
56
57
58
100 µm
25 µm
100 µm

Figs. 53–58. *Proctolaelaps certator:* 53, female dorsum; 54, female venter; 55, female spermathecal system; 56, male dorsum; 57, male venter; 58, male chelicera.

setae r2–6 and R1–6 on edge of shield, R7 on membrane posterior to shield; 3 pairs of submarginal setae (UR) on lateral membrane posteriad of coxae IV. The following measurements of dorsal setae were taken from the holotype: j1 a stout spine, 33 μm long; j2, z1, s1, and J5 shorter than other dorsal setae, about 8–11 μm; most other dorsal setae subequal, 13–15 μm, Z5 a stout spine, 106 μm; marginal setae longer than most dorsal setae, gradually increasing in length from anterior to posterior, r3 (24 μm) only slightly longer than r2 (22 μm); R7 longer than others (59 μm). Glands, proprioceptors, and muscle scars positioned as indicated in Figure 53.

Venter (Fig. 54) very similar to *P. belemensis* except region of sternal shield anterior to first sternal setae lineate and with a pair of distinct pre-endopodal sclerites; genital shield more elongate and tapering anteriorly. Posterior ventral setae Jv4 and Jv5 elongate and spinelike, 63 and 88 μm long. Spermathecal system (Fig. 55) simple, consisting of an adductor canal wider nearer to external opening, approximately 145 μm long; a very short, bulbous maturation pouch at inner terminus of canal; and a very short, hooked spermiduct. Gnathosoma and legs as in *P. belemensis*.

MALE (Figs. 56–58).—Idiosomal length 500 (486–509), width 320 (313–351) μm ($n = 10$). Linear-reticulate pattern covering dorsal shield (Fig. 56). Shield with 44 pairs of setae, all marginal setae on shield except R7. One pair of submarginals (UR1) laterad of coxae IV. Relative lengths of dorsal setae as in female; j1-35, r3-29, R7-41, Z5-78 μm; most other dorsal setae 13–18 μm. Glands, proprioceptors, and muscle scars as shown in Figure 56.

Venter (Fig. 57) with tritosternum shorter than in female. A pair of small presternal sclerites adjacent to genital opening. Sternogenital shield with reticulate pattern well developed over entire shield except anteriomedially, with 5 pairs of setae and 3 pairs of pores. Ventrianal shield widened anteriorly, incorporating metapodal plates, reticulated over entire surface, with 6 pairs of ventral setae on shield, Jv1–3, Zv1–3, in addition to paraanal setae; setae Jv4–5 on membrane; Jv5 a thickened spine, 64 μm long; other setae filiform, relative lengths as in female. Paraanal setae relatively short (22 μm), postanal seta a thickened spine 51 μm long. Peritremes as in female, extending anteriad to the vicinity of seta z1. Endopodal apodemes fused to sternogenital shield; exopodal sclerites well developed laterad of coxae.

Gnathosoma with tectum as in female, broadly triangular and strongly toothed. Chelicerae with fixed digit with a large, subapical tooth and a row of fine teeth, membranous, bidentate process on paraxial surface; movable digit strongly hooked, with a subapical tooth. Arthrodial membrane at base of movable digit strongly fimbriate. Spermatodactyl slightly curving distally, projecting posterioventrally, 180–185 μm long; other features of gnathosoma as on female.

Legs I–IV (excluding pretarsi) 108, 81, 82, and 106% of dorsal shield length. Coxae with linear ornamentation as in female. Legs generally similar to female except some setae shorter and more spinelike; these include av1 of femur I, av1 of femur II, av and pv of genu II, and pv of genu III. Ventral seta of femur IV enlarged, but with movable articulation. Pretarsi all elongate.

ETYMOLOGY.—The specific name *certator* is from the Latin meaning "disputant" and is a masculine noun in apposition.

MATERIAL EXAMINED.—Holotype female from flowers of *Heliconia bihai* L. (Musaceae), Andrews Trace, 10 mi N Arima, 21 February 1976, R. K. Colwell (#U60) (holotype and 3 paratype females); the following collections also from *H. bihai* (all paratypes): Simla Research Station, 4 mi N Arima, 15 February 1976, R. K. Colwell (#U59) (1 female, figured and 1 other male); same locality, March 1980, D. S. Dobkin (#9) (4 females); same data (#18) (2 females); same data (#26) (2 females, 6 males); same data (#28) (3 females, 2 males); same data (#45) (2 females, 3 males); Waller Field, 22 February 1976, R. K. Colwell (#U63) (1 female, 1 male).

The following collections from flowers of *Heliconia tortuosa* Griggs (Musacaeae): Temple Village, Davis Home Road, 11 March, 1980; D. S. Dobkin (#T533) (2 females, 2 males); Simla Research Station, March 1980, D. S. Dobkin (#53) (1 female).

The following specimens from flowers of *Aechmea fendleri* Andre (Bromeliaceae): top of Arima Valley, Textel Road, 1 March 1979, R. K. Colwell (#T252) (3 females).

The following specimens from flowers of *Costus scaber* Ruiz & Pavón (Zingiberaceae):

Andrews Trace, 10 mi N Arima, 1 August 1975, R. K. Colwell (#T7) (4 females); La Laja Trace, 8 mi N Arima, 23 February 1976, R. K. Colwell (#U33) (2 females, 1 male); near Simla Research Station, 4 mi N Arima, 11 June 1976, P. Feinsinger (#W16) (6 females); same locality, 12 August 1975, R. K. Colwell (#T59) (2 females).

SPECIMEN DEPOSITION.—Holotype and paratypes in UMMZ, other paratypes in BYU, NMNH, CNC, IRSNB.

COMMENTS.—One of four relatively large species in the *belemensis*-group, this species is very similar if not identical to *P. cyanocompsae*. The latter species was only diagnosed with reference to *P. belemensis*; the character states listed as diagnostic also occur in *P. certator* and *P. contentiosus* (see below). The only measurements given for *P. cyanocompsae* were idiosomal length and width, and these values fall within the range of *P. certator* as described above. We were unable to examine the holotype of *P. cyanocompsae*, and until this specimen or additional material from the type-locality can be described in better detail, or males are discovered, the relationship between *P. cyanocompsae* and *P. certator* cannot be resolved with certainty.

Proctolaelaps contentiosus, new species

Proctolaelaps contentiosus Colwell, 1986: 408, nomen nudum

Proctolaelaps contentiosus Heyneman et al., 1990: 467, nomen nudum.

DIAGNOSIS.—This species is very similar to *P. certator*. Females (Figs. 59–61) differ primarily in the distinctly larger body size (idiosomal length 702, 726, [684–784], width 486, 516 [468–626] μm; dorsal shield length 626, 621 [585–644], width 468, 469 [427–486] μm [$n = 10$]), the greater length of anterior marginal seta r3 compared with other anterior marginal setae (r3 1.25–1.5 times the length of r2 and r4), and the greater length of posterior ventral seta Jv5 (1.7 times the length of Jv4, vs. 1.2–1.4 in *P. certator*).

MALE (Figs. 62–64).—Similar to *P. certator* but larger, idiosomal length 534 (527–544), width 361 (331–392) μm ($n = 4$). Anterior marginal seta r3 enlarged as in female; posterior ventral region with setae Zv3 usually absent (unilaterally present in 1 of 4 specimens, absent in all others); posterior ventral seta Jv4 shorter than Jv2. Spermatodactyl (Fig. 64) distinctly shorter than in *P. certator*, length 160–165 μm.

ETYMOLOGY.—The specific name *contentiosus* is from the Latin meaning "given to combat."

MATERIAL EXAMINED.—All specimens were collected from flowers of *Renealmia exaltata* L. f. (Zingiberaceae) as follows: La Laja Trace, 8 mi N Arima, 8 August 1975, R. K. Colwell (#T55) (holotype and one other female, 2 males); same locality, 5 August 1975, R. K. Colwell (#T16) (6 females); same locality, 23 February 1976, R. K. Colwell (#U52) (figured male); La Laja Plantation, 2 March 1979, R.K. Colwell (#T258) (2 females, 2 males).

SPECIMEN DEPOSITION.—Holotype and paratypes in UMMZ, other paratypes in BYU, USNM, CNC.

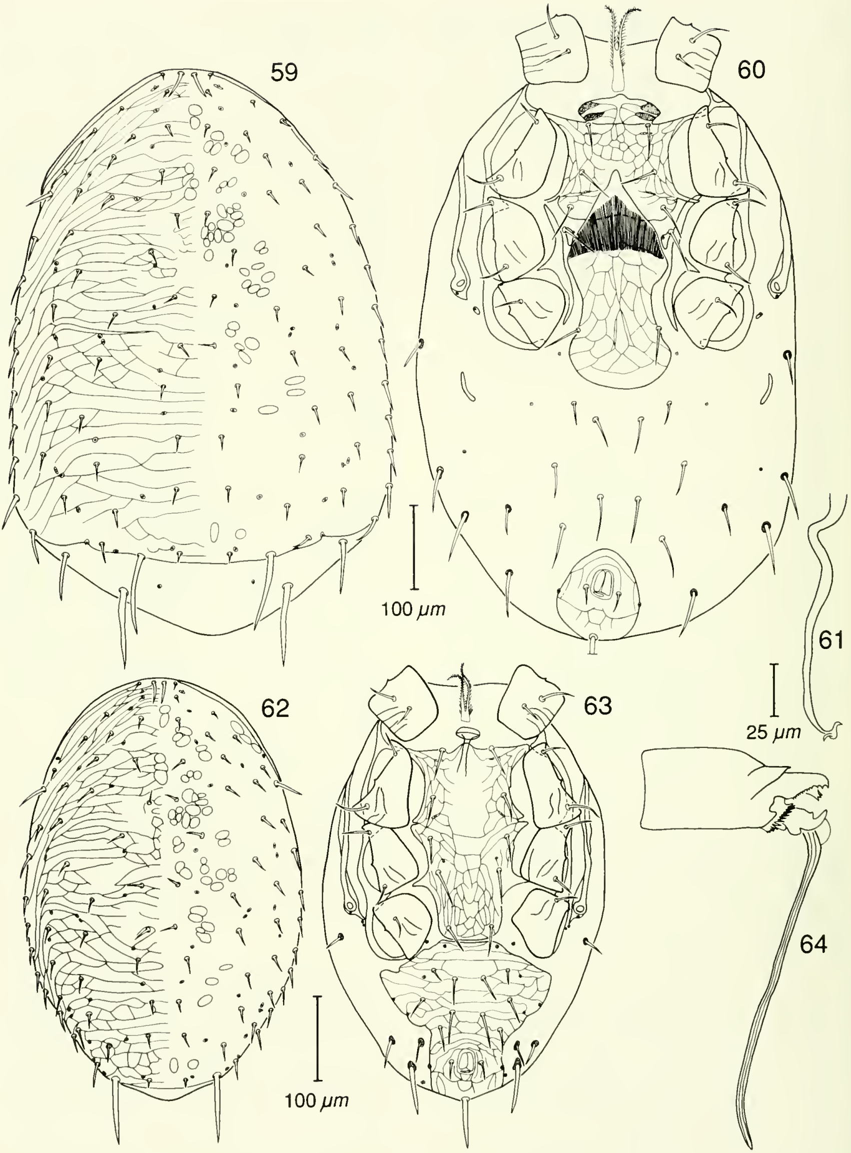
COMMENTS.—*Proctolaelaps contentiosus* is the largest species now known in the *belemensis*-group. It may be distinguished from *P. certator* by the different length proportions described above. It is interesting to note that although males are absolutely larger than in *P. certator*, the spermatodactyl length is distinctly shorter in *P. contentiosus*. We have found spermatodactyl length in species of the *belemensis*-group to show little within-species variation, but differences between species are marked.

Key to the Species of Flower-inhabiting *Proctolaelaps* in Trinidad

1. Both sexes with dorsal setae j1 stout and spinelike, 2.5–3 times longer than setae j2; female with anterior edge of genital plate strongly tapering; male with spinelike ventral seta of femur IV articulating directly with segment, not on an enlarged process; male leg setae otherwise simple, without expanded, bulbous bases . . . . *belemensis*-group 6

Both sexes with dorsal setae j1 similar in length to setae j2, rarely somewhat enlarged (*P. rabulatus*); female with anterior edge of genital plate broadly rounded; male with spinelike ventral seta of femur IV fused to an enlarged process of the segment; male with some ventral setae of tarsus II, genu and tibia IV with expanded, bulbous bases . . . . *kirmsei*-group 2

2. Female with anterior lobes of sternal shield narrowly connected to shield; anterior lobes without linear pattern; female with a pair of very small paragenital setae off shield laterad of genital setae; male with ventrianal shield widened anteriorly, without separate metapodal plates; male with all dorsal shield setae (except Z5)


59
60
100 μm
61
25 μm
62
63
64
100 μm

Figs. 59–64. *Proctolaelaps contentiosus:* 59, female dorsum; 60, female venter; 61, female spermathecal system; 62, male dorsum; 63, male venter; 64, male chelicera.

relatively short, not longer than the distances between the setae . . . . *rabulatus*

Female with anterior lobes broadly connected to sternal shield, lobes with linear pattern; female without paragenital setae; male ventrianal shield parallel-sided, metapodal plates large and distinct; male with some dorsal setae enlarged and spinelike, much longer than the distance to the next posterior seta 3

3. Female with metasternal setae on platelets; male with central dorsal setae (j5–6 and J1, z5–6 and Z1, s5–6 and S1) very large and spinelike, and posterior dorsal and marginal setae (except Z5) all very short (S2–3 similar in length to S5) 4

Female with metasternal setae on membranous cuticle, metasternal platelets absent; male with central dorsal setae variably formed, and with some posterior and/or marginal setae very large and spinelike (S2–3 at least twice as long as S5) 5

4. Both sexes with dorsal seta j2 similar in length to j1; female with maturation pouch of spermathecal system very short, only slightly longer than wide; male with dorsal setae z2, z3, and s3 very short, not longer than distance to next posterior seta . . . . *kirmsei*

Both sexes with dorsal seta j2 approximately twice as long as j1; female with maturation pouch of spermathecal system about 2.5 times longer than wide; male with dorsal setae z2, z3 and s3 enlarged and spinelike, longer than the distance to the next posterior seta . . . . *jurgatus*

5. Both sexes with dorsal setae z3 absent; female with all marginal setae except r2–3 off the dorsal shield, posterior submarginal (UR) setae and ventral seta Jv4 long and spinelike, longer than distance to next posterior seta; male with 3 pairs of posterior marginal setae (R1–3) enlarged and spinelike, longer than adjacent setae S1–3, other posterior marginal setae (R4–7) absent . . . . *mermillion*

Both sexes with dorsal setae z3 present; female with all marginal setae except R7 on dorsal shield, posterior submarginal setae and ventral seta Jv4 shorter than distance to next posterior seta; male with at least 5 pairs of posterior marginal setae, all posterior marginals relatively short; posterior setae S2–3 very large and spinelike, at least 5 times longer than adjacent marginal setae R2–3 . . . . *glaucis*

6. Female dorsal shield length less than 480 μm; male spermatodactyl length 100–105 μm . . . . *contumex*

Female dorsal shield length greater than 520 μm; male spermatodactyl length greater than 130 μm 7

7. Female dorsal shield length 585–644 μm; male spermatodactyl length 160–165 μm . . . . *contentiosus*

Female dorsal shield length less than 585 μm, male spermatodactyl length greater than 170 or less than 150 μm 8

8. Female with anterior marginal seta r3 distinctly longer than adjacent marginal setae r2 and r4; male spermatodactyl length 180–185 μm . . . *certator*

Female with anterior marginal seta r3 similar in length to r2 and r4; male spermatodactyl length 140 μm . . . . *belemensis*

ACKNOWLEDGMENTS

We were assisted in the collection of specimens in Trinidad by David S. Dobkin, Amy Heyneman, and Peter Feinsinger. Accommodations were provided by the Asa Wright Nature Center, Jack Price, station manager. Dr. Alex Fain, then of the Prince Leopold Institute for Tropical Medicine, Antwerp, Belgium, graciously provided specimens of described species for comparison. Margaret Lentell and Robert Naczi helped prepare specimens. The late June OConnor prepared most of the original illustrations, and Margaret van Bolt prepared the plates. Dr. Marek Kaliszewski, Brigham Young University, reviewed the manuscript. Grant support for this study was provided by the National Science Foundation (DEB 78-12038 and BSR 8906228) to RKC.

LITERATURE CITED

COLWELL, R. K. 1979. The geographical ecology of hummingbird flower mites in relation to their host plants and carriers. Pages 461–468 *in* J. G. Rodriguez, ed., Recent advances in acarology. Vol 2. Academic Press, New York.

_____. 1985. Stowaways on the hummingbird express. Natural History 94:56–63.

_____. 1986a. Community biology and sexual selection: lessons from hummingbird flower mites. Pages 406–424 *in* J. Diamond and T. J. Case, eds., Community ecology. Harper & Row, New York.

_____. 1986b. Population structure and sexual selection for host fidelity in the speciation of hummingbird flower mites. Pages 475–495 *in* S. Karlin and E. Nevo, eds., Evolutionary processes and theory. Academic Press, New York.

DOBKIN, D. S. 1984. Flowering patterns of long-lived *Heliconia* inflorescences: implications for visiting and resident nectarivores. Oecologia 64:245–254.

_____. 1985. Heterogeneity of tropical floral microclimates and the response of hummingbird flower mites. Ecology 66:536–543.

DOMROW, R. 1979. Ascid and ameroseiid mites phoretic on Australian mammals and birds. Records of the Western Australian Museum 8:97–116.

DOWNES, B. J. 1990. Host-induced morphology in mites: implications for host-parasite coevolution. Systematic Zoology 39: 162–168.

EBERHARD, W. G. 1985. Sexual selection and animal genitalia. Harvard University Press, Cambridge. 244 pp.

FAIN, A., K. E. HYLAND, AND T. H. G. AITKEN. 1977a. Nouveaux acariens Ascidae (Mesostigmates) phorétiques dans les fosses nasales de colibris (Note préliminaire). Bulletin et Annales de la Société royale Belgique d'Entomologie 113:184–186.

_____. 1977b. Flower mites of the family Ascidae phoretic in nasal cavities of birds (Acari: Mesostigmata). Acta Zoologica et Pathologica Antverpiensia 69: 99–154.

FEINSINGER, P., AND R. K. COLWELL. 1978. Community organization among Neotropical nectar-feeding birds. American Zoologist 18:779–795.

HEYNEMAN, A. J., R. K. COLWELL, S. NAEEM, D. S. DOBKIN, AND B. HALLET. 1990. Host plant discrimination: experiments with hummingbird flower mites. Pages 455–485 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, eds., Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons, New York.

HYLAND, K. E., A. FAIN, AND A. S. MOORHOUSE. 1978. Ascidae associated with the nasal cavities of Mexican birds (Acarina: Mesostigmata). Journal of the New York Entomological Society 86:260–267.

KARG, W. 1985. Die Raubmilbengattung *Proctolaelaps* Berlese, 1923. Zoologischer Jahrbucher, Systematik 112: 185–206.

LINDQUIST, E. E. 1971. New species of Ascidae (Acarina: Mesostigmata) associated with forest insect pests. Canadian Entomologist 103:919–942.

NAEEM, S., D. S. DOBKIN, AND B. M. OCONNOR. 1985. *Lasioseius* mites (Acari: Gamasida: Ascidae) associated with hummingbird-pollinated flowers in Trinidad, West Indies. International Journal of Entomology 27:338–353.

OCONNOR, B. M., R. K. COLWELL AND S. NAEEM. In preparation. The flower mites of Trinidad III. The genus *Rhinoseius* (Acari: Ascidae).

RYKE, P. A. J. 1954. Two new predatory mites (Acarina: Phytoseiidae) from *Proteas* in the Western Province. Journal of the Entomological Society of South Africa 17:241–245.

_____. 1964. Acarina associated with *Protea* flowers in the Cape Province. Journal of the Entomological Society of South Africa 26: 337–354.

Received 25 September 1990
Accepted 12 July 1991

Great Basin Naturalist 51(4), 1991, pp. 377–396

OXYTROPIS DC.—NAMES, BASIONYMS, TYPES, AND SYNONYMS—FLORA NORTH AMERICA PROJECT

Stanley L. Welsh[1]

ABSTRACT.— All names known to apply to the genus *Oxytropis* de Candolle in North America are listed with place of publication, type information (where known), type specimen repositories, and notations pertinent to understanding the nomenclatural aspects of the genus. Nomenclatural combinations proposed are: *Oxytropis arctica* R. Brown var. *murrayi* (Jurtzev) Welsh and *O. campestris* (L.) de Candolle var. *roaldii* (Ostenfeld) Welsh.

Key words: Oxytropis, *North America, names, types, synonyms.*

Preparation of a revisionary summary of the genus *Oxytropis* de Candolle for the Flora North America Project necessitates that nomenclatural changes and type information be presented prior to publication in that project. The following list consists of synonyms, names, nomenclatural types, and new combinations of names involved with this interesting and complex genus as it occurs in North America. Each name involved with the genus is listed with its bibliographical citation, type information, places of deposit of the types, and other pertinent information as necessary.

All names cited in the literature are included. In some few of them the place of deposition of the type is unknown, and the space for that information is left blank. *Oxytropis* consists of some 57 taxa in 22 species in its North American complement. The taxonomic problems are disproportionate with the size of the genus, however. The large number of synonyms reflects the problematic nature of the taxa within the genus. Further complicating the number of names have been the nomenclatural transfers to earlier published genera *Aragallus* Neck. and *Spiesia* Neck. The conservation of *Oxytropis* DC. forestalled ultimate adoption of either of those generic names. Some authors, Tidestrom for example, discerned the close relationship of *Oxytropis* with *Astragalus* L., and he subsequently made wholesale transfers of the names to that genus. While having considerable merit from a phylogenetic standpoint, the inclusion would have further burdened an already huge genus and overlooked the divergence of the oxytropes from most of the astragalus complexes. In North America only the introduced *O. riparia* and the indigenous *O. deflexa* are caulescent or have caulescent phases. The porrect beak of the keel is diagnostic for the genus, even though some species of *Astragalus* have extended keel apices; none are truly porrect.

Aside from the problem of nomenclatural transfers, which have added to the list of synonyms, the main difficulties are morphological; there are few consistent morphological features to serve as taxonomic criteria. The pods, with some exceptions, are mainly alike, especially in those taxa that are most alike otherwise. The flowers are similar through the genus, the main differences being in size (and that varies greatly within some species) and color (which also varies within a species and often within the infraspecific categories). The taxonomist has had to rely on features of stipules, leaves, inflorescence, pubescence, and calyx or pod inflation to arrive at a treatment that still lacks absolute consistency. Morphological intermediates, resulting from hybridization or from overlap of widely varying characteristics, tend to cloud the picture. Chromosome number is helpful, to an extent, but plants with differing ploidy levels are known within species and some of the varieties; and chromosome number is not always associated with other morphological features.

---

[1] Life Science Museum and Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

Some workers have looked at the genus as if the taxa were clear and distinctive, resulting in the proliferation of specific and infraspecific names. Each new morphological variant was considered worthy of a name by some students of the genus. Adding to the difficulties of interpretation of taxonomic and nomenclatural problems was the circumboreal nature of the genus. In Alaska and other northern regions of North America, some species were clearly allied closely to Siberian or Eurasian taxa. A paucity of critical materials from Siberia for comparison with the American counterparts made interpretation difficult. Specimens from Siberia in American herbaria are still the exception. In the *campestris* and *borealis* complexes the need for such comparisons is critical. Both species were named prior to any of the North American counterparts, and it was not until the critical review of *Oxytropis* by Barneby (1952) that clarification of many of the problems became a possibility, although the equivalence was discerned earlier by Gray (1884) and others. Much additional work and refinement of the infraspecific taxa in the complexes with circumboreal representation is necessary.

The present writer has examined all but a few of the taxa in the field and has spent almost three decades in their pursuit. It is hoped that this summary of names will be helpful. Works of special importance to this paper include those by Barneby (1952), Boivin (1962, 1967), Bunge (1874), Elisens and Packer (1980, 1982), Gray (1884), Jurtsev (1986), Porsild and Cody (1980), Vasil'chenko et al. (1948), and Welsh (1967, 1974, 1977, and 1987).

***Aragallus abbreviatus* Greene,** Proc. Biol. Soc. Wash. 18: 12. 1905.
Type: Texas, near Dallas, Limestone prairie, Dallas County, J. Reverchon 603, May 1876; holotype NDG!; isotype NY!; dry calcareous soil near Dallas, Texas, Curtis 603, April, May; cotype GH!, NDG!, NY!
= *Oxytropis lambertii* Pursh var. *articulata* (Greene) Barneby

***Aragallus aboriginum* Greene,** Proc. Biol. Soc. Wash. 18: 12. 1905.
Type: Oklahoma, Cimarron Valley, Cherokee Outlet, M. N. Carleton 217, June 1891; holotype US!, photo BRY!
= *Oxytropis sericea* Nuttall var. *sericea*

***Aragallus albertinus* Greene,** Proc. Biol. Soc. Wash. 18: 15. 1905.
Type: Saskatchewan, Prince Albert, Lat. 53°, J. M. Macoun 12535 and 12540, July 1896; cotypes NDG!
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Aragallus albiflorus* A. Nelson,** Erythea 7: 62. 1899, nom. nov.
Basionym: *Oxytropis lambertii* Pursh var. *ochroleuca* A. Nelson
= *Oxytropis sericea* Nuttall var. *sericea*

var. *condensatus* A. Nelson, Erythea 7: 62. 1899.
Type: Wyoming, Bitter Creek, Red Desert, Sweetwater County, A. Nelson 4773, 16 June 1898; holotype RM!; isotypes NY!, US!
= *Oxytropis sericea* Nuttall var. *sericea*

***Aragallus alpicola* Rydberg,** Mem. N. Y. Bot. Gard. 1: 252. 1900.
Type: Montana, Old Hollowtop near Pony [South Boulder Range, Madison County], P. A. Rydberg & E. Bessey 4503, 9 July 1897; holotype NY!; isotypes GH!, NDG!, US!, NY!
= *Oxytropis campestris* (L.) de Candolle var. *cusickii* (Greenman) Barneby

***Aragallus angustatus* Rydberg,** Bull. Torrey Bot. Club 34: 422. 1907.
Type: Nebraska, Rush Creek, Duel County, P. A. Rydberg 82c, 2 July 1891; holotype NY!; isotypes MIN!, NEB!
= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus arcticus* (R. Brown) Greene,** Pittonia 3: 211. 1897.
Basionym: *Oxytropis arctica* R. Brown
= *Oxytropis arctica* R. Brown

***Aragallus argophyllus* Rydberg,** Mem. N. Y. Bot. Gard. 1: 255. 1900.
Type: Little Blackfeet River, Montana, J. G. Cooper s.n., 1860; holotype NY!; isotype GH! (frag), US!
= *Oxytropis besseyi* (Rydberg) Blankinship var. *argophylla* (Rydberg) Barneby

***Aragallus articulatus* Greene,** Proc. Biol. Soc. Wash. 18: 13. 1905.
Type: Between Fort Smith and the Rio Grande [Oklahoma or western Texas], J. M. Bigelow s.n., 1853; holotype US!
= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus atropurpureus* Rydberg,** Bull. Torrey. Bot. Club 34: 424. 1907.
Type: Headwaters of the Tongue River, Big Horn Mountains, Wyoming; F. Tweedy 125, 126, 1898; cotypes NY!
= *Oxytropis lagopus* Nuttall var. *atropurpureus* (Rydberg) Barneby

***Aragallus aven-nelsonii* Lunell,** Bull. Leeds Herb. 2: 6. 1908.
Type: North Dakota, Butte, Benson County, J. Lunell s.n., 14, 21 June, 2 July 1908; isotypes NY!, US!, WTC, MIN!, NDA!
= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus bellii* (Britton) Greene,** Pittonia 3: 212. 1897.
Basionym: *Spiesia Oxytropis bellii* Britton
= *Oxytropis arctica* R. Brown var. *bellii* (Britton) Boivin

***Aragallus besseyi* Rydberg,** Mem. N. Y. Bot. Gard. 1: 250. 1900.

Type: Montana, Spanish Basin, Gallatin County, 6,500 ft., P. A. Rydberg & E. A. Bessey 4501, 23 June 1897; holotype NY!; isotypes GH!, NDG!, US!

= *Oxytropis besseyi* (Rydberg) Blankinship var. *besseyi*

***Aragallus bigelovii* (A. Gray) Greene,** Pittonia 3: 212. 1897.

Basionym: *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray

= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus blankinshipii* A. Nelson,** Erythea 7: 58. 1899.

Type: Montana, dry rocky hillsides along Middle Creek, 15 mi SW of Bozeman, Gallatin County, J. W. Blankinship s.n., 4 July 1898; holotype RM!; isotypes GH!, NY!

= *Oxytropis lagopus* Nuttall var. *lagopus*

***Aragallus bryophilus* Greene,** Proc. Biol. Soc. Wash. 18: 17. 1905.

Type: Alaska, St. Matthew Island, J. M. Macoun 18510, 10 July 1891; holotype NDG!

= *Oxytropis nigrescens* (Pallas) Fischer var. *nigrescens*

***Aragallus campestris* (L.) de Candolle var. *johannensis* Fernald ex Macoun,** Ottawa Nat. 13: 163. 1899, nomen.

Basionym: *Oxytropis campestris* (L.) de Candolle var. *johannensis* Fernald

= *Oxytropis campestris* (L.) de Candolle var. *johannensis* Fernald

***Aragallus caudatus* Greene,** Pittonia 4: 69. 1899.

Type: Saskatchewan, Moose Jaw, J. M. Macoun 13957, 26 June 1896; holotype NDG!; isotype CAN!

= *Oxytropis splendens* Douglas

***Aragallus cervinus* Greene,** Proc. Biol. Soc. Wash. 18: 16. 1905.

Type: British Columbia, Deer Park, Lower Arrow Lake, J. M. Macoun 5358, 8 June 1890; holotype NDG!

= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Aragallus collinus* A. Nelson,** Erythea 7: 57. 1899.

Type: Wyoming, Seminoe Mts., Carbon County, E. Nelson 4925, 21 July 1898; holotype RM!; isotypes GH!, NY!, US!

= *Oxytropis nana* Nutt.

***Aragallus deflexus* (Pallas) A. A. Heller,** Cat. N. Amer. Pl., 4. 1898.

Basionym: *Astragalus deflexus* Pallas

= *Oxytropis deflexa* (Pallas) de Candolle

***Aragallus dispar* A. Nelson,** Erythea 7: 61. 1899.

Type: North Dakota, Dickinson, Stark County, Mrs. Cook s.n., 1896; holotype RM!; photo BRY!

= *Oxytropis campestris* (L.) de Candolle var. *dispar* (A. Nelson) Barneby

***Aragallus falcatus* Greene,** Proc. Biol. Soc. Wash. 18: 13. 1905.

Type: Missouri, Watson, Atchison County, B. F. Bush 204, 1 June 1894; holotype NDG!; isotypes GH!, NY!, US!, ISC!, MIN!, MO!, DAO! (Note: The same collection is also the type of *Oxytropis bushii* Gandoger.)

= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus foliolosus* (Hooker) Macoun,** Ottawa Naturalist 13: 163. 1899.

Basionym: *Oxytropis foliolosa* Hooker

= *Oxytropis deflexa* var. *foliolosa* (Hooker) Barneby

***Aragallus formosus* Greene,** Proc. Biol. Soc. Wash. 18: 13. 1905.

Type: South Dakota, Fort Meade, Meade County, W. H. Forwood 95, 7 June 1887; holotype US!, photo BRY!

= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus galioides* Greene,** Proc. Biol. Soc. Wash. 18: 16. 1905.

Type: Alberta, Bow River near Banff, McCalla s.n., 10 July, 18 September 1899; holotype US!

= *Oxytropis splendens* Douglas

***Aragallus gracilis* A. Nelson,** Erythea 7: 60. 1899.

Type: Wyoming, Limestone Range, Newcastle, Weston County, A. Nelson 2545, 30 July 1896; holotype RM!; isotypes GH!, NY!, US!

= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Aragallus hallii* (Bunge) Rydberg,** Bull. Torrey Bot. Club 33: 144. 1906.

Basionym: *Oxytropis hallii* Bunge

= *O. podocarpa* A. Gray

***Aragallus hudsonicus* Greene,** Proc. Biol. Soc. Wash. 18: 17. 1905.

Type: Canada, Whale River, Hudson Bay; A. P. Low 14272, 24 June 1896; holotype NDG!; isotype GH!, S!

= *Oxytropis borealis* de Candolle var. *hudsonica* (Greene) Welsh

The specimen at Stockholm has information identical to that at GH, except that the collection is attributed to Spreadborough.

***Aragallus inflatus* (Hooker) A. Nelson,** Erythea 7: 59. 1899.

Basionym: *Oxytropis arctica* δ *inflata* Hooker

= *Oxytropis podocarpa* A. Gray

***Aragallus invenustus* Greene,** Proc. Biol. Soc., Wash. 18: 12. 1905.

Type: South Dakota, about Fort Meade, Meade County, W. H. Forwood 96a, 96b, 3 June 1887, 96b, 7 June 1887; cotypes US!, photo BRY!

= *Oxytropis sericea* Nuttall var. *sericea*

***Aragallus involutus* A. Nelson,** Erythea 78: 64. 1899.

Type: Minnesota, Acton, Meeker County, W. D. Frost s.n., June 1892; holotype RM!; isotypes MIN!, MO!, US!

= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus johannensis* (Fern.) A. Heller,** Cat. N. Amer. Pl., ed 2: 7. 1900.

Basionym: *Oxytropis campestris* (L.) de Candolle var. *johannensis* Fernald

= *Oxytropis campestris* (L.) de Candolle var. *johannensis* Fernald

***Aragallus knowltonii* Greene,** Proc. Biol. Soc. Wash. 18: 12. 1905.

Type: Arizona, San Francisco Mountains, Coconino County, F. H. Knowlton 44, 20 August 1889; holotype US!

= *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray

***Aragallus lagopus* (Nuttall) Greene**, Pittonia 3: 212. 1897.
Basionym: *Oxytropis lagopus* Nuttall

***Aragallus lambertii* (Pursh) Greene**, Pittonia 3: 212. 1897.
Basionym: *Oxytropis lambertii* Pursh

var. *sericeus* (Nuttall) A. Gray, Proc. Amer. Acad. 20: 7. 1884.
Basionym: *Oxytropis sericea* Nuttall

***Aragallus luteolus* Greene**, Proc. Biol. Soc. Wash. 18: 17. 1905.
Type: Washington, Olympic Mts., Clallam County, A. D. Elmer 2532, July 1900; holotype US!; isotypes NE, NY!, NDG!, MIN!, MO!, WTC, CAS!, DS!
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Aragallus majusculus* Greene**, Proc. Biol. Soc. Wash. 18: 12. 1905.
Type: Utah, Henry Mts., Garfield County, Utah, M. E. Jones 5674, July 1894; holotype US!; isotype NY!, MO!, photo BRY!
= *Oxytropis sericea* Nuttall var. *sericea*

***Aragallus macounii* Greene**, Proc. Biol. Soc. Wash. 18: 16. 1905.
Type: Alberta, Elbow River, Rocky Mountains, Lat. 49°40′, J. M. Macoun 18517, June–July 1897; holotype NDG!
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby
Two specimens, J. M. Macoun 18516 and 18517, were cited as type of *Aragallus macounii* Greene. Barneby (1952) designated 18517 as the type of the taxon; the other specimen belongs to *O. sericea* Nuttall var. *spicata* (Hooker) Barneby.

***Aragallus melanodontus* Greene**, Proc. Biol. Soc. Wash. 18: 15. 1905.
Type: Alberta, Elbow River, Rocky Mountains, Lat. 49°40′, J. M. Macoun 18513, June-July 1897; holotype NDG!
= *Oxytropis sericea* Nuttall var. *spicata* (Hooker) Barneby

***Aragallus mertensianus* (Turczaninow) Greene**, Pittonia 3: 211. 1897.
Basionym: *Oxytropis mertensiana* Turczaninow
= *Oxytropis mertensiana* Turczaninow

***Aragallus metcalfei* Greene**, Proc. Biol. Soc. Wash. 18: 12. 1905.
Type: New Mexico, Sawyer's Peak, Grant County, open glade, ca 10,000 ft., O. B. Metcalf 1079, 7 July 1904; holotype US!; isotypes NY!, CAS!, GH!, POM, WTC.
= *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray

***Aragallus minor* (A. Gray) Cockerell ex Daniels**, Univ. Missouri Sci. Stud. II, 2: 158. 1911.
Basionym: *Oxytropis multiceps* var. *minor* A. Gray
= *Oxytropis multiceps* Torrey & Gray

***Aragallus monticola* (A. Gray) Greene**, Pittonia 3: 212. 1897.
Basionym: *Oxytropis monticola* A. Gray
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Aragallus multiceps* (Torrey & Gray) A. Heller**, Cat. N. Amer. Pl., 4. 1898.
Basionym: *Oxytropis multiceps* Torrey & Gray
= *Oxytropis multiceps* Torrey & Gray

var. *minor* (A. Gray) A. Nelson, Erythea 7: 57. 1899.
Basionym: *Oxytropis multiceps* var. *minor* A. Gray
= *Oxytropis multiceps* Torrey & Gray

***Aragallus nanus* (Nuttall) Greene**, Pittonia 3: 212. 1897.
Basionym: *Oxytropis nana* Nuttall
= *Oxytropis nana* Nuttall

***Aragallus oreophilus* (A. Gray) A. Nelson**, Erythea 7: 59. 1899.
Basionym: *Oxytropis oreophila* A. Gray
= *Oxytropis oreophila* A. Gray

***Aragallus parryi* (A. Gray) Greene**, Pittonia 3: 211. 1897.
Basionym: *Oxytropis parryi* A. Gray
= *Oxytropis parryi* A. Gray

***Aragallus patens* Rydberg**, Bull. Torrey Bot. Club 34: 421. 1907.
Type: Colorado, plains and foothills near Boulder, Boulder County, F. Tweedy 5164, 1902; holotype NY!
= *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray

***Aragallus pinetorum* A. Heller**, Bull. Torrey Bot. Club 26: 548. 1899.
Type: New Mexico, 11 mi SE of Santa Fe, Santa Fe County, A. A. & E. G. Heller 3751, 23 June 1897; holotype US! (?); isotypes MO!, IA!, MU!, GH!, NDG!, NY!, POM, WTC, BRY!, DS!
= *Oxytropis sericea* Nuttall var. *sericea*

var. *veganus* Cockerell, Torreya 2: 155. 1902.
Type: New Mexico, top of Las Vegas Range, on end of ridge, T. D. A. Cockerell 20, end of June 1901; holotype NY!; isotype GH!
= *Oxytropis sericea* Nuttall var. *sericea*

***Aragallus plattensis* Nuttall ex Torrey & Gray**, Fl. N. Amer. 1: 340. 1838
Type: ?
= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus podocarpus* (A. Gray) A. Nelson**, Coulter & Nelson, New Man., 294. 1909.
Basionym: *Oxytropis podocarpa* A. Gray
= *Oxytropis podocarpa* A. Gray

***Aragallus richardsonii* (Hooker) Greene**, Pittonia 4: 69. 1899.
Basionym: *Oxytropis splendens* β *richardsonii* Hooker
= *Oxytropis splendens* Douglas

***Aragallus rigens* Greene**, Proc. Biol. Soc. Wash. 18: 14. 1905.
Type: Montana, Cedar Creek, 12 mi above Glendive, Dawson County, L. F. Ward s.n., 15 July 1884; holotype US!, photo BRY!
= *Oxytropis lambertii* Pursh var. *lambertii*

***Aragallus saximontanus* A. Nelson**, Erythea 7: 190. 1899, nom. nov.
Basionym: *Oxytropis lambertii* Pursh var. *ochroleuca* A. Nels.
= *Oxytropis sericea* Nuttall var. *sericea*

var. *condensatus* (A. Nelson) A. Nelson, Erythea 7: 190. 1900.

Basionym: *Aragallus albiflorus* var. *condensatus* A. Nelson

= *Oxytropis sericea* Nuttall var. *sericea*

Aragallus sericeus **(Nuttall) Greene,** Pittonia 3: 212. 1897.

Basionym: *Oxytropis sericea* Nuttall

= *Oxytropis sericea* Nuttall

Aragallus spicatus **(Hooker) Rydberg,** Mem. N. Y. Bot. Gard. 1: 251. 1900.

Basionym: *Oxytropis campestris* δ *spicata* Hooker

= *Oxytropis sericea* Nuttall var. *spicata* (Hooker) Barneby

Aragallus splendens **(Douglas) Greene,** Pittonia 3: 211. 1897.

Basionym: *Oxytropis splendens* Douglas

= *Oxytropis splendens* Douglas

Aragallus varians **Rydberg,** Bull. N. Y. Bot. Gard. 2: 176. 1901.

Type: Yukon, Lewes River, J. B. Tarleton 33b, 28 June 1899; holotype US!; isotypes S!, NY!

= *Oxytropis campestris* (L.) de Candolle var. *varians* (Rydberg) Barneby

Aragallus veganus **(Cockerell) Wooton & Standley,** Contr. U. S. Nat. Herb. 16: 136. 1913.

Basionym: *Aragallus pinetorum veganus* Cockerell

= *Oxytropis sericea* Nuttall var. *sericea*

Aragallus ventosus **Greene,** Proc. Biol. Soc. Wash. 18: 15. 1905.

Type: Dry ground in the valley of the North Fork of Wind River, Wyoming, W. H. Forwood 65, 12 July 1884; holotype US!; isotype GH!

= *Oxytropis besseyi* (Rydberg) Blankinship var. *ventosa* (Greene) Barneby

Aragallus villosus **Rydberg,** Bull. Torrey. Bot. Club 28: 36. 1901.

Type: Montana, Craig, Lewis and Clark County, E. N. Wilcox 378, 20 June 1900; holotype US!; isotype NY!

= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

Aragallus viscidulus **Rydberg,** Mem. N. Y. Bot. Gard. 1: 253. 1900.

Type: Montana, Melrose, Silver Bow County, P. A. Rydberg 2716, 6 July 1895; holotype NY!

= *Oxytropis borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. *depressus* **Rydberg,** Mem. N. Y. Bot. Gard. 1: 253. 1900.

Type: Haystack Mt., Stillwater County, Montana, F. Tweedy 120; holotype NY!

= *Oxytropis borealis* de Candolle var. *viscida* (Nuttall) Welsh

Aragallus viscidus **(Nuttall) Greene,** Pittonia 3: 211. 1897.

Basionym: *Oxytropis viscida* Nuttall

= *Oxytropis borealis* de Candolle var. *viscida* (Nuttall) Welsh

Astragalus albertinus **(Greene) Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937.

Basionym: *Aragallus albertinus* Greene

= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

Astragalus albiflorus **(A. Nelson) Gandoger,** Bull. Soc. Bot. France 48: xiv. 1901.

Basionym: *Aragallus albiflorus* A. Nelson

= *Oxytropis sericea* Nuttall var. *sericea*

Astragalus alpicola **(Rydberg) Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937.

Basionym: *Aragallus alpicola* Rydberg

= *Oxytropis campestris* (L.) de Candolle var. *cusickii* (Greenman) Barneby

Astragalus arcticus **(R. Brown) Sprengel,** Syst. 4: 288. 1827.

Basionym: *Oxytropis arctica* R. Brown

= *Oxytropis arctica* R. Brown

Astragalus bellii **(Britton) Tidestrom,** Proc. Biol. Soc. Wash. 50: 18. 1937.

Basionym: *Spiesia bellii* Britton

= *Oxytropis arctica* R. Brown var. *bellii* (Britton) Boivin

Astragalus biflorus **Schweinitz ex Gray,** Proc. Amer. Acad. 6: 234. 1864, synonym.

= *Oxytropis podocarpa* A. Gray

Astragalus bisontum **Tidestrom,** Proc. Biol. Soc. Wash. 50: 18. 1937.

= *Oxytropis multiceps* Torrey & Gray

var. *minor* **(A. Gray) Tidestrom,** Proc. Biol. Soc. Wash. 50: 18. 1937.

Basionym: *Oxytropis multiceps* var. *minor* A. Gray

= *Oxytropis multiceps* Torrey & Gray

Astragalus blankinshipii **(A. Nelson) Tidestrom,** Proc. Biol. Soc. Wash. 50: 18. 1937.

Basionym: *Aragallus blankinshipii* A. Nelson

= *Oxytropis lagopus* Nuttall

Astragalus campestris **L.,** Sp. Pl., 761. 1753.

Type: "in Oelandia, Germania, Helvetia"; holotype LINN 926/51!

= *Oxytropis campestris* (L.) de Candolle

Astragalus coronaminis **(Fernald) Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1947.

Basionym: *Oxytropis coronaminis* (Fernald) Tidestrom

= *Oxytropis arctica* R. Brown var. *arctica*

Astragalus deflexus **Pallas,** Acta Acad. Sci. Imp. Petrop. 2: 268. 1779.

Type: "ad nivalia Dauriae . . . circa Balyra rivum aliosque Ononem influentibus" [Siberia], P. S. Pallas s.n.; holotype BM.

= *Oxytropis deflexa* (Pallas) de Candolle var. *deflexa*

var. *foliolosus* **(Hooker) Tidestrom,** Proc. Biol. Soc. Wash. 50: 18. 1937.

Basionym: *Oxytropis foliolosa* Hooker

= *Oxytropis deflexa* (Pallas) de Candolle var. *foliolosa* (Hooker) Barneby

Astragalus gaspensis **(Fernald & Kelsey) Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937.

Basionym: *Oxytropis gaspensis* Fernald & Kelsey

= *Oxytropis borealis* de Candolle var. *viscida* (Nuttall) Welsh

Astragalus grayanus **Tidestrom, in Tidestrom & Kittell,** Fl. Ariz. & New Mex., 216. 1941, nom. nov.

= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Astragalus lagopus* (Nuttall) Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937.
Basionym: *Oxytropis lagopus* Nuttall
= *Oxytropis lagopus* Nuttall

***Astragalus lambertii* (Pursh) Sprengel,** Syst. 3: 308. 1826.
Basionym: *Oxytropis lambertii* Pursh
= *Oxytropis lambertii* Pursh var. *lambertii*

var. *bigelovii* (A. Gray) Tidestrom, Proc. Biol. Soc. Wash. 50: 19. 1937.
Basionym: *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray
= *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray

***Astragalus mazama* (St. John) G. N. Jones,** Univ. Wash. Pub. Bot. 7: 175. 1938.
Basionym: *Oxytropis mazama* St. John.
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Astragalus munzii* Wheeler,** Leafl. W. Bot. 2: 209. 1939, nom. nov.
= *Oxytropis oreophila* A. Gray

***Astragalus nigrescens* Pallas,** Astragalogia, 65, tab. 53. 1800.
Type: "inter Aldanum fl[umen] et orientalem Oceanum" [between Aldan River and the Sea of Okhotsk, Siberia], D. D. Merk; type LE.
= *Oxytropis nigrescens* (Pallas) de Candolle

var. *arctobia* (Pallas) Tidestrom, Proc. Biol. Soc. Wash. 50: 19. 1937.
Basionym: *Oxytropis arctobia* Pallas
= *Oxytropis nigrescens* var. *uniflora* (Hooker) Barneby

***Astragalus oreophilus* (A. Gray) Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937.
Basionym: *Oxytropis oreophila* A. Gray
= *Oxytropis oreophila* A. Gray

***Astragalus parryanus* Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1941.
nom. nov. pro *Oxytropis parryi* A. Gray
= *Oxytropis parryi* A. Gray

***Astragalus pygmaeus* Pallas,** Astragalogia, 66, tab. 54. 1800.
Type: ?
= *Oxytropis nigrescens* (Pallas) Fischer var. *nigrescens*

***Astragalus retroflexus* Pallas,** Astragalogia, 33, tab. 27. 1800.
Type: ?
= *Oxytropis deflexa* var. *deflexa*

***Astragalus rusbyi* Green & Morris,** J. Amer. Soc. Agron. 27: 546, 549, figs. 1, 2. 1935, prov. nom.
= *Oxytropis riparia* Litvinov

***Astragalus rydbergianus* Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937, nom. nov.
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Astragalus saximontanus* (A. Nelson) Tidestrom, in Tidestrom & Kittell,** Fl. Ariz. New Mex., 216. 1941.
Basionym: *Aragallus saximontanus* A. Nelson, nom. nov. *Oxytropis lambertii* Pursh var. *ochroleuca* A. Nelson
= *Oxytropis sericea* Nuttall var. *sericea*

***Astragalus septentrionalis* Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937, substitute name.
= *Oxytropis podocarpa* A. Gray

***Astragalus splendens* (Douglas) Tidestrom,** Proc. Biol. Soc. Wash. 50: 18. 1937.
Basionym: *Oxytropis splendens* Douglas
= *Oxytropis splendens* Douglas

var. *richardsonii* (Hooker) Tidestrom, Proc. Biol. Soc. Wash. 50: 128. 1937.
Basionym: *Oxytropis splendens* β *richardsonii* Hooker
= *Oxytropis splendens* Douglas

***Astragalus tomae* Tidestrom,** Proc. Biol. Soc. Wash. 50: 18. 1937, nom. nov.
= *Oxytropis nana* Nuttall

***Astragalus viscidus* (Nuttall) Tidestrom,** Proc. Biol. Soc. Wash. 50: 19. 1937.
Basionym: *Oxytropis viscida* Nuttall
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

***Oxytropis alaskana* A. Nelson,** Univ. Wyo. Pub. Bot. 1: 120. 1926.
Type: Kachemak Bay, Cook Inlet, M. W. Gorman 1560; holotype RM!; isotype WTU.
= *O. campestris* (L.) de Candolle var. *varians* (Rydberg) Barneby

***Oxytropis albertina* (Greene) Rydberg,** Fl. Prair. & Pl., 484. 1932.
Basionym: *Aragallus albertinus* Greene
= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Oxytropis albiflora* (A. Nelson) K. Schumann,** Just's Bot. Jahresb. 27: 496. 1901.
Basionym: *Aragallus albiflorus* A. Nelson, nom. nov. *Oxytropis lambertii* Pursh var. *ochroleuca* A. Nelson
= *O. sericea* Nuttall var. *sericea*

***Oxytropis alpicola* (Rydberg) M. E. Jones,** Mont. Bot. Notes, 34. 1910.
Basionym: *Aragallus alpicola* Rydberg
= *O. campestris* (L.) de Candolle var. *cusickii* (Greenman) Barneby

***Oxytropis angustata* (Rydberg) A. Nelson,** Univ. Wyo. Pub. Bot. 1: 116. 1926.
Basionym: *Aragallus angustatus* Rydberg
= *O. lambertii* var. *lambertii*

***Oxytropis arctica* R. Brown,** Parry's First Voy., Append. 9: 278. 1824.
Type: Canada, Melville Island, Parry's First Voyage, Sabine, Edwards, Ross, and others, 1819–1820; holotype (?) S!; isotype GH!

var. *arctica*
Distribution: Alaska, Yukon, Canadian Arctic Archipelago, N.W.T. east to north of Hudson Bay, and less commonly in the interior.

The var. *arctica* is recognizable by its racemes of mainly fewer than 8 large purple or lavender flowers on plants mainly less than 15 cm tall and leaflets not or seldom fasciculate. Mainly they occur in or near coastal Alaska and Canada; less commonly they are montane plants of the interior or occur in other interior situations.

var. ***barnebyana*** **Welsh,** Great Basin Nat. 28: 152, fig. 4. 1968.

Type: Alaska, Kotzebue, 66°55′N, 162°40′W, S.L. Welsh 5729, 1966; holotype BRY!; isotype NY!, UC!

Distribution: Coastal northwestern Alaska; endemic.

Flower size, pilose stipules, and calyx features indicate an alliance to the sympatric *O. arctica*. The racemes vary from subcapitate to somewhat expanded. In the expanded form the plants are a close match for much of *O. arctica* in a strict sense. The placement of *O. arctica* var. *barnebyana* with *O. sordida*, a taxonomic entity considered by European authors (see Flora Europaea) at infraspecific level within *O. campestris*, has considerable merit. However, the treatment of var. *barnebyana* at infraspecific level within *O. sordida*, a highly variable taxonomic entity with both pale and colored flowers, by Jurtsev (1986), does not solve the basic problem of the similarity of *barnebyana* to *O. arctica*, however well that placement indicates the similarity of this North American phase with the protean *campestris* complex. The calyx teeth of var. *barnebyana* vary from short, as in some phases of *O. campestris*, to almost as long as in some phases of *O. arctica*. The sympatry of *O. arctica* and the allopatry of *O. campestris*, while not conclusive, weigh in the decision to keep the Kotzebue materials of var. *barnebyana* with *O. arctica*. And, the lack of a stopping place for additional inclusions of North American taxa within expanded versions of *campestris* or *sordida* is likewise a consideration.

ssp. ***bellii*** **(Macoun) Love & Love,** Taxon 31: 347. 1982.

Basionym: *Spiesia bellii* Britton ex Macoun

= *O. arctica* R. Brown var. *bellii* (Britt.) Boivin

var. ***bellii*** **(Britton) Boivin,** Naturaliste Canad. 94: 73. 1967.

Basionym: *Spiesia bellii* Britton ex Macoun

Distribution: Kewatin, vicinity of Hudson Bay, Canada; endemic.

The similarity of this large-flowered low plant of coastal or near coastal Hudson Bay and vicinity to specimens designated as var. *murrayi* is readily apparent. They also simulate closely plants from Armatkchene Island off the coast of Siberia. The latter are evidently included by Jurtsev (1986) as portions of an expanded *O. sordida*. The alliance of var. *bellii* to *O. arctica* has long been recognized. Any expansion of *O. sordida* to include it would also, logically, include the remainder of the *arctica* complex. Such a proposal is herein considered as both illogical and unnecessary.

δ ***inflata*** **Hooker,** Fl. Bor.-Amer., 1: 146. 1834.

Type: "Without locality, '*O. arctica* comm. Hooker'"; holotype ?; isotypes GH!, NY!, PH!

= *O. podocarpa* A. Gray

The specimen at GH! is accompanied by a small label bearing the notation, "O. arctica δ inflata." Below it in Asa Gray's handwriting is the note, "O. podocarpa. Plenty and same with the rather inflated legume in Hb. Kew." Below that, in the writing of a person not identified, is the notation, "Highest summits of the Rocky Mts., Drummond." The plant is almost certainly typical material of var. *inflata*.

var. ***koyukukensis*** **(Porsild) Welsh,** Iowa State J. Sci. 41: 280. 1967.

Basionym: *O. koyukukensis* Porsild

Distribution: Umiat, Wiseman, Anaktuvuk, Koyukuk, Shatolik, and Northway vicinities, Alaska; endemic.

The specimens upon which this variety are based vary considerably. They tend to be tall plants with several flowered racemes, but they approach if not actually pass into var. *arctica* (specimens from Anaktuvuk). Leaflet arrangement ranges from entire to fasciculate to merely scattered. To the south they simulate specimens of var. *murrayi*, described by Jurtsev (1986) in *O. sordida*.

var. ***murrayi*** **(Jurtsev) Welsh** comb. nov.

Basionym: *O. sordida* var. *murrayi* Jurtsev Arctic Fl. U.S.S.R. 9(2): 179. 1986.

Distribution: St. Elias Mts., SW Yukon, Canada; endemic.

This taxon is the portion of the *arctica* complex most similar to var. *bellii*, from which it is distantly isolated, but is probably most nearly allied to the nearer disjunct, var. *koyukukensis*. Robust materials of var. *murrayi* closely simulate some of var. *koyukukensis*. The differences between vars. *murrayi* and *bellii* rest on such intangibles as the apparently larger flowers, broader calyces with mixed shaggy villous vesture, and tendency to larger leaflets of var. *murrayi*.

α ***subumbellata*** **Hooker,** Parry's Second Voy., Append. 4: 396. 1825.

Type: ?

= *O. arctica* R. Brown var. *arctica*

β ***uniflora*** **Hooker,** Parry's Second Voy., Append. 4: 396. 1825.

Type: Barrow River, E coast Melville Peninsula, lat. 67°21′N, on Parry's Second Voyage; isotypes GH!, NY!

= *O. nigrescens* (Pallas) Fischer var. *uniflora* (Hooker) Barneby

varietas notabilis, **R. Brown,** Chlor. Melvill., 254. 1823.

= *O. nigrescens* (Pallas) Fischer var. *uniflora* (Hooker) Barneby

Oxytropis arctobia **Bunge,** Gen. Oxytropis, 114. 1874.

Type: ?

= *O. nigrescens* (Pallas) Fischer var. *uniflora* (Hooker) Barneby

var. ***hyperarctica*** **Polunin,** Bot. Canad. E. Arctic, 293, pl. 8. 1940.

Type: Franklin district, Baffin Island, Arctic Bay, N. Polunin 2583, 8–11 Sept. 1936; holotype CAN; isotypes GH!, BM, OXF.

= *O. nigrescens* (Pallas) Fischer var. *uniflora* (Hooker) Barneby

Oxytropis atropurpurea **(Rydberg) A. Nelson,** Univ. Wyo. Pub. Bot. 1: 117. 1928.

Basionym: *Aragallus atropurpureus* Rydberg

= *Oxytropis lagopus* Nuttall var. *atropurpurea* (Rydberg) Barneby

***Oxytropis aven-nelsonii* (Lunell) A. Nelson,** Univ. Wyo. Pub. Bot. 1: 116. 1926

Basionym: *Aragallus aven-nelsonii* Lunell

= *Oxytropis lambertii* Pursh var. *lambertii*

***Oxytropis bellii* (Britton) Palibin,** Bull. Soc. Bot. Geneve II, 2: 19. 1910.

Basionym: *Spiesia bellii* Britton

= *O. arctica* R. Brown var. *bellii* (Britton) Boivin

***Oxytropis besseyi* (Rydberg) Blankinship,** Mont. Agric. Coll. Sci. Stud. Bot. 1: 80. 1904.

Basionym: *Aragallus besseyi* Rydberg

var. *argophylla* (Rydberg) Barneby, Leafl. W. Bot. 5: 111. 1951.

Basionym: *Aragallus argophyllus* Rydberg

Distribution: W Montana, adjacent Idaho, and NE Nevada.

var. *besseyi*

Distribution: Idaho, Montana, Wyoming, and Saskatchewan.

var. *fallax* Barneby, Proc. Calif. Acad. Sci. IV, 27: 235. 1952.

Type: Clay slope among boulders, 4350 ft., mouth of Shell Creek, Big Horn Mountains, Big Horn County, Wyoming, 4,350 ft., H. D. Ripley & R. C. Barneby 8010, 16 June 1946; holotype CAS!; isotypes GH!, US!, RM!

Distribution: West of the Bighorn River, Wyoming.

var. *obnapiformis* (C. L. Porter) Welsh, Great Basin Nat. 38: 337. 1978.

Basionym: *O. obnapiformis* C. L. Porter

Distribution: NW Colorado, NE Utah, and SW Wyoming.

The pod of this variety is strictly sessile or nearly so, not stipitate as in other phases of the species with inflated pods. Plants from the type locality near Mayfield, Colorado, have 13–25 leaflets and inflorescences about equaling the leaves. Those from Daggett County, Utah, have 5–9 leaflets and inflorescences surpassing the leaves. Plants from elsewhere bridge the two phases.

var. *salmonensis* Barneby, Proc. Calif. Acad. Sci. IV, 24: 234. 1952.

Type: Salmon River Canyon, 12 mi below Clayton, Custer County, Idaho, alt. 5,400 ft., H. D. Ripley & R. C. Barneby 8829, 22 June 1947; holotype CAS!; isotypes NY!; IDS.

Distribution: Custer Co., Idaho; endemic.

var. *ventosa* (Greene) Barneby, Leafl. W. Bot. 5: 111. 1951.

Basionym: *Aragallus ventosus* Greene

Distribution: S Montana, W Wyoming, and NE Utah.

***Oxytropis bilocularis* A. Nelson,** Univ. Wyo. Pub. Bot. 1: 114. 1926

Type: Arizona, high moist slopes, Miller Peak, Huachuca Mts., Cochise County, L. N. Goodding 2411, 22 August 1907; holotype RM!; isotypes GH!, NY!, UC!, POM.

= *O. lambertii* var. *bigelovii* A. Gray

***Oxytropis blankinshipii* (A. Nelson) K. Schumann,** Just's Bot. Jahresb. 27: 496. 1901.

Basionym: *Aragallus blankinshipii* A. Nelson

= *O. lagopus* Nuttall var. *lagopus*

***Oxytropis borealis* de Candolle,** Prodromus 2: 275. 1825.

Type locality: "In terra Tschuktschorum ad sinum Sancti-Laurentii," collector not stated. Type: "e sinu S. Laurentii in terra Tsuchuktschorum (pays des Tchouktchi) septentrionem versus a fretus Beringii. Legumina divisa a leg. ox. montana. m. Fischer 1825"; G-DC.!

= *O. borealis* de Candolle var. *borealis*

var. *australis* Welsh, Great Basin Nat. 50: 359. 1991.

This southern phase of *O. borealis* is mainly montane in distribution, but occurs mostly on xeric sites in sagebrush, black sagebrush, grass, ponderosa pine, and aspen parkland communities, often on exposed ridges or outcrops. Main substrate types are of igneous origin, either granitic or basaltic derived soils, but limestone also serves as a substrate. Elevational range varies from 2135 to 3355 m.

Distribution: Inyo and Mono counties, California, Nevada, and S Utah.

β Hooker & Arnott, Bot. Beechey Boy., 122. 1832.

Type: ?

= *Oxytropis borealis* de Candolle var. *borealis*

var. *borealis*

Distribution: N.W.T., Yukon, and Alaska; Chukotsk.

The relatively few leaflets, ample flowers, and condensed, copiously hirsute inflorescence in combination allow this entity to be rather readily identified. It consists, at least in part, of what has passed under the name of *O. glutinosa* Porsild, who excluded the type of "*subsucculenta*" from consideration in treatment of the genus in "Vascular Plants of Continental Northwest Territories Canada" (Porsild & Cody 1979). Included within the concept of var. *borealis* is the *O. uralensis* β *subsucculenta* Hooker, the basis of *O. viscida* var. *subsucculenta* (Hooker) Barneby.

var. *hudsonica* (E. Greene) Welsh, Great Basin Nat. 50: 357. 1991.

Basionym: *Aragallus hudsonicus* E. Greene, Proc. Biol. Soc. Wash. 18: 17. 1905.

Distribution: Yukon east to Hudson Bay.

This is the phase of the species that occurs in North America mainly east of the Yukon, but with some representation in that province, where it is transitional with both var. *viscida* and var. *sulphurea*.

var. *sulphurea* (Porsild) Welsh, Great Basin Nat. 50: 358. 1991

Basionym: *Oxytropis viscidula* ssp. *sulphurea* Porsild, Bull. Nat. Mus. Can. 121: 247. 1951. Includes: *O. verruculosa* Porsild.

Distribution: British Columbia, Yukon, and E Alaska.

These are the pallid-flowered plants of the Yukon and Alaska. In their most typical condition the racemes are compactly and uniformly small flowered. They vary from that norm to elongate racemes with small to large flowers. The bracts are mainly small, but in some they are very long and conspicuous in the inflorescence. On the one side the plants seem to grade with var. *hudsonica* and on the other with both var. *viscida* and var. *borealis*.

var. *viscida* (Nuttall) Welsh, Great Basin Nat. 50: 359. 1991.

Basionym: *O. viscida* Nuttall, ex Torrey & Gray, Flora N. Amer. 1: 341. 1838.

Distribution: Alaska, Yukon, N.W.T., Gaspe, British Columbia, Alberta, Minnesota, Oregon, Idaho, Wyoming, Nevada, Utah, Colorado, and California.

This variety includes almost as much diversity as the species as a whole. The numerous subunits are held together by tenuous characteristics that are difficult to define or place in a key. Variation is often great in populations from adjacent hillsides or on a single gravel bar, especially in the Arctic. One is reminded of the conditions of morphological variation occurring in the boreal *O. nigrescens* var. *nigrescens*, as treated by this author. Unless one is willing to support a taxonomy wherein the purported taxa are largely sympatric and consist of morphological subunits whose genetic continuity is questionable, made up of a series of similar plants held together by that similarity and not by genetic linkage, there does not seem to be a reasonable way to segregate the morphological variation as taxa. The rather large number of synonyms, often at specific or varietal level, reflects the attempts at segregation.

***Oxytropis bushii* Gandoger,** Bull. Soc. Bot. France 48: xvii. 1901.

Type: Missouri, Watson, Atchison County, B. F. Bush 204, 7 June 1894; isotypes GH!, NDG, ISC! NY!, US!, MIN!, MO!

= *O. lambertii* var. *lambertii*

***Oxytropis campestris* (L.) de Candolle,** Astragalogia, 59. 1802.

Basionym: *Astragalus campestris* L.

var. *americana* Brunet, Cat. Pl. Canad., 39. 1865, nomen.

= *O. campestris* (L.) de Candolle var. *johannensis* Fernald

var. *cervinus* (Greene) Boivin, Naturaliste Canad. 94: 75. 1967.

Basionym: *Aragallus cervinus* Greene

= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

var. *chartacea* (Fassett) Barneby, Proc. Calif. Acad. IV, 27: 269. 1952.

Basionym: *O. chartacea* Fassett

Distribution: Known only from lake shores in central and NW Wisconsin; endemic.

Plants with other of the syndrome of characteristics of var. *johannensis* in Ontario (Farm River area) also have short pods as in var. *chartacea*. These have not been examined in the field, and it seems best not to relegate this otherwise Wisconsin endemic to synonymy until more study has been completed.

var. *columbiana* (St. John) Barneby, Leafl. W. Bot. 5: 111. 1951.

Basionym: *O. columbiana* St. John

Distribution: Columbia River above the mouth of the Spokane River, NE Washington (where possibly extirpated), and forested margin of Flathead Lake, Montana.

This variety is characterized by its white to ochroleucous flowers with maculate keel tips and soft pubescence. It is still extant at Flathead Lake.

var. *cusickii* (Greenman) Barneby, Leafl. W. Bot. 5: 111. 1951.

Basionym: *O. cusickii* Greenman

Distribution: British Columbia, Alberta, Washington, Oregon, Idaho, Montana, Wyoming, Utah, and Colorado.

This taxon is highly variable in flower size, especially where the large-flowered *O. sericea* var. *spicata* occurs nearby. Transitionally apparent populations again demonstrate the lack of consistent diagnostic features to separate what are otherwise distinctive populations. The same problem is apparent where var. *gracilis* occurs nearby at lower elevations than these montane phases of the *campestris* complex (see also var. *varians*).

var. *davisii* Welsh, Leafl. W. Bot. 10: 25. 1963.

Type: British Columbia, mi 403.4, Alaska Hwy, R. J. Davis 6076, 19 July 1962; holotype BRY!; isotype IDS!

Distribution: SW Alberta, NE British Columbia.

This plant is readily distinguished by its colorful flowers, fasciculate leaflets or tendency to fasciculate leaflets, and elongate inflorescences. Specimens have been known in collections from early times, but have been regarded as occasional intermediates between portions of the *campestris* complex and *O. borealis* var. *viscida*, or, they have been identified, because of the fasciculate leaflets, as *O. splendens*. The plants are locally abundant on stream gravels and adjacent slopes in the foothills mainly of the Alberta Rockies and in northeast British Columbia. The plants form apparent intermediates with var. *gracilis*.

var. *dispar* (A. Nelson) Barneby, Leafl. W. Bot. 5: 111. 1951.

Basionym: *Aragallus dispar* A. Nelson

Distribution: North Dakota and Manitoba.

Plants of this variety are closely allied to var. *gracilis*, from which they differ in the flowers being polychrome in populations, and in the somewhat firmer texture of the pods. It may well be that var. *dispar* is the somewhat stabilized product of previous hybridization involving the mainly disjunct pale-flowered var. *gracilis* and the now far disjunct purple-flowered vars. *davisii* and *johannensis*. Purple-flowered or polychrome populations or entire taxa within the *campestris* complex are now known to be at least as important as are the pale-flowered phases. Indeed, pink-purple flowers show up here and there throughout North America, even in otherwise white or ochroleucous populations.

var. ϵ *glabrata* Hooker, Fl. Bor.-Amer. 1: 147. 1834.

Type: Bear Lake to the Arctic Shores and Islands [possibly Richardson]; isotype (?) GH!

= *O. maydelliana* Trautvetter

ssp. *gracilis* (A. Nelson) Boivin, Naturaliste Canad. 94: 74. 1967

Basionym: *Aragallus gracilis* A. Nelson

= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

var. *gracilis* (A. Nelson) Barneby, Leafl. W. Bot. 5: 111. 1951.

Basionym: *Aragallus gracilis* A. Nelson

Distribution: Mainly south of the 65th parallel in British Columbia, Alberta, Saskatchewan, Manitoba, Washington, Montana, Wyoming, South Dakota, North Dakota, and Colorado.

This is a highly variable taxon whose morphological subunits have been regarded by some previous workers as belonging to several specific or infraspecific taxa. A portion of the problem revolves around the inclusion of materials with two different base chromosome numbers, 32 and 48. At least some portion of it is the southern counterpart of var. *varians*, which is reported to have the base chromosome number of 48. The variety is transitional to var. *davisii* in southwestern Alberta, to var. *dispar* in North Dakota, and more especially to the montane var. *cusickii*, which often occurs at the tops of the same mountains whose bases bear var. *gracilis*.

var. ***johannensis*** **Fernald,** Rhodora 1: 88. 1899.

Type: Maine, gravelly shores, valley of St. John River, Fort Kent, Aroostook County, M. L. Fernald 2289, 15 June 1898; holotype GH!; isotype CAN!, US!, NY!

Distribution: Newfoundland, New Brunswick, Nova Scotia, Quebec, Ontario, and Maine.

Plants of this variety from the Farm River area, south of James Bay, Ontario, have fasciculate leaflets and short pods. In the latter feature they simulate the var. *chartacea*, which might best be regarded as only a disjunct phase of this variety.

ssp. ***jordalii*** **(Porsild) Hulten,** Ark. Bot. 7: 79. 1967.

Basionym: *O. jordalii* Porsild

= *O. campestris* (L.) de Candolle var. *jordalii* (Porsild) Welsh

var. ***jordalii*** **(Porsild) Welsh,** Leafl. W. Bot. 10: 25. 1963.

Basionym: *O. jordalii* Porsild

Distribution: N Alaska, N Yukon, and N.W.T. Mackenzie District.

This is a dwarf boreal variety of ridge tops, gravel bars, and arctic tundra with small white to ochroleucous flowers. It is easily recognizable in its typical phases, but it passes by degree, especially in lower elevation and more mesic sites into var. *varians*. On some gravel bars, especially, the plants are transitional with the other dwarf boreal var. *roaldii*. It is with the latter variety, with pink-purple flowers, that it seems to be most closely allied.

var. ***ξ melanocephala*** **Hooker,** Fl. Bor.-Amer. 1: 147. 1834.

Type: Bear Lake to the Arctic Shores and Islands [possibly Richardson]; isotype (?) GH.

= *O. maydelliana* Trautvetter

var. ***roaldii*** **(Ostenfeld) Welsh,** comb. et stat. nov.

Basionym: *O. roaldii* Ostenfeld, Vasc. pl. Arct. N. Amer. Gjoa Exped., 54, pl. 3, fig. 16. 1910.

Distribution: N Alaska, N Yukon, and adjacent N.W.T.

The type of this variety was included in the synonymy of *O. arctica* by Barneby (1952), whose experience with boreal representatives was limited by the few specimens available to him. The type specimen was taken on Herschell Island on the Amundsen Gjoa Expedition and is clearly the same as plants that occur inland in northern Yukon Territory and west in Alaska to Prudhoe Bay and beyond. The variety is characterized by its small pink-purple flowers and other features that simulate and pass into the partially sympatric var. *jordalii*. The var. *roaldii* further simulates and is probably allied to the eastern var. *terrae-novae*.

var. ***rydbergii*** **(A. Nelson) R. J. Davis,** Madrono 11: 144. 1951.

Basionym: *O. rydbergii* A. Nelson

= *O. campestris* (L.) de Candolle var. *cusickii* (Greenman) Barneby

β speciosa **Torrey & Gray,** Fl. N. Amer. 1: 341. 1838.

Type: "Dr. Hooker" NY!. See Flora Boreali-Americana 1: 147. 1833. "Carleton House Saskatchewan to Rocky Mts. [T.] Drummond." The sheet at NY bears the notation quoted above and the initials E. P. S[heldon].

= *O. sericea* Nuttall var. *spicata* (Hooker) Barneby

δ spicata **Hooker,** Fl. Bor.-Amer. 1: 174. 1834.

Type: Between Carlton House on the Saskatchewan and the Rocky Mountains [Alberta], T. Drummond s.n.; holotype ?; ? isotypes GH, NY!

= *O. sericea* Nuttall var. *spicata* (Hooker) Barneby

var. ***terrae-novae*** **(Fernald) Barneby,** Proc. Calif. Acad. IV, 27: 266. 1952.

Basionym: *O. terrae-novae* Fernald

Distribution: Hudson Bay, Baffin Island, Ungava Peninsula, Labrador, and coastal Newfoundland.

Reports of this taxon from the Mackenzie Mountains are probably of the purple-flowered var. *roaldii*, which is a western vicariad of var. *terrae-novae* that differs in minor but consistent ways. At Churchill, Manitoba, there is a mixture of specimens variously assigned to vars. *varians*, *terrae-novae*, or *johannensis*. They should be viewed in the field prior to an attempt to resolve their relationships.

var. ***varians*** **(Rydberg) Barneby,** Proc. Calif. Acad. IV, 27: 253. 1952.

Basionym: *Aragallus varians* Rydberg

Distribution: Alaska, Yukon, N.W.T., N Manitoba, and N British Columbia, mainly north of the 65th parallel.

Plants of this variety are highly variable, with numerous differing morphological phases often growing together on the same gravel bar in portions of Alaska and the Yukon. Alpine portions of the variety, especially in SW Yukon, N British Columbia, and adjacent SE Alaska, closely simulate high-altitude materials of *O. campestris* var. *cusickii* at its northern limits in S British Columbia and Alberta. Indeed, there are specimens of *O. campestris* var. *gracilis*, the so called "*cervinus*" phase in southern British Columbia, that almost match the "*alaskana*" materials of var. *varians* from southern Alaska. The maintenance of var. *varians* as separate from var. *gracilis* rests mainly on allopatry and historical perspective. Specimens of var. *varians* appear to intergrade with those of var. *jordalii* in montane sites near Juneau, Alaska.

var. ***verrucosa*** **Ledebour,** Fl. Ross. 1: 591. 1842.

Type: "in terra Tschuktschorum ad sinum Sancti-Laurentii," collector not stated, but probably

based on the type of *O. borealis* (q.v.).
= *O. borealis* de Candolle var. *borealis*

var. *viscida* (Nuttall) S. Watson, U.S. Geol. Expl. 40th Parallel, Bot. 5: 55. 1871.
Basionym: *O. viscida* Nuttall
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. *wanapum* Joyal, Great Basin Naturalist 50: 373. 1991.
Type: Washington, Saddle Mt. above Lower Carb Creek, E. Joyal 12643, 25 May 1987; holotype US!; isotypes BRY!, ISC!, OSU!
Distribution: Known only from the type locality.
This is a plant of xeric, basaltic talus; the flowers suffused with purple are diagnostic, since no other phases of the genus in the Pacific Northwest typically have colored flowers. The narrow leaflets tend to be involute and to vary in number from 20 to 25. These vegetative features are unlike any of the other several varieties of *O. campestris* that occur elsewhere in North America having lavender to purplish flowers.

***Oxytropis cascadensis* St. John,** Proc. Biol. Soc. Wash. 41: 105. 1928.
Type: Washington, Grouse Creek, Mt. Baker, Whatcom County, St. John 5513; holotype WTC!; photo BRY!
= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Oxytropis caudata* (Greene) K. Schumann,** Just's Bot. Jahresb. 27: 496. 1901.
Basionym: *Aragallus caudatus* Greene
= *O. splendens* Douglas

***Oxytropis chartacea* Fassett,** Rhodora 38: 95. 1936.
Type: Wisconsin, sandy shore of Lake Huron, Plainfield, Waushara County, N. C. Fassett 16704, 15 Sept. 1936; holotype WIS!; isotypes GH!, ISC!, MO!, IA!, GH!, NY, MU!, NY!, PH!, US!, UC!, DAO!
= *O. campestris* (L.) de Candolle var. *chartacea* (Fassett) Barneby

***Oxytropis collina* (A. Nelson) K. Schumann,** Just's Bot. Jahresb. 27: 496. 1901.
Basionym: *Aragallus collinus* A. Nelson
= *O. nana* Nuttall

***Oxytropis columbiana* St. John,** Proc. Biol. Soc. Wash. 41: 100. 1928.
Type: Gravelly beach of the Columbia River, Marcus, Stevens County, H. St. John 6482, 27 June 1924; holotype WTC; isotype GH!
= *O. campestris* (L.) de Candolle var. *columbiana* (St. John) Barneby

***Oxytropis condensata* (A. Nelson) A. Nelson,** Univ. Wyo. Pub. Bot. 1: 115. 1926.
Basionym: *Aragallus albiflorus* var. *condensatus* A. Nelson
= *O. sericea* Nuttall var. *sericea*

***Oxytropis coronaminis* Fernald,** Rhodora 30: 151, pl. 175. 1928.
Type: Mackenzie, Arctic sea-coast, Dr. Richardson s.n.; holotype GH!
= *Oxytropis arctica* R. Brown var. *arctica*

***Oxytropis cusickii* Greenman,** Erythea 7: 116. 1899.
Type: Oregon, alpine summits of the Wallowa Mountains, W. C. Cusick 1365, 2095, 23 August 1886; lectotype (Elisens & Packer, Canad. J. Bot. 58: 1827. 1980) GH!; Cusick 2095, Aug. 1898, syntypes GH!, NY!, NDG!, UC, US!
= *O. campestris* (L.) de Candolle var. *cusickii* (Greenman) Barneby

***Oxytropis czukotica* Jurtsev,** Bull. Mosk. Obtz. Icp. Prir., Otd. Biol. 85. 6: 102. 1980.
nom. nov. pro *O. tschuktschorum* Jurtsev
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

***Oxytropis deflexa* (Pallas) de Candolle,** Astragalogia, 33, tab. 27. 1802.
Type: "ad nivalia juga Dauria . . . in excelsis montibus circa balyra rivum aliosque Ononem influentibus" [Siberia], S. P. Pallas s.n.; holotype BM.

var. *capitata* Boivin, Svensk Bot. Tidskr. 56: 499. 1962.
Type: Ontario, cordon gazonnant le long d'une riviere, 34 mi au sud du cap Henriette, 44°54′N, A. Dutilly & E. Lepage 34367, 17 Aout 1953; holotype DAO!
= *O. deflexa* var. *foliolosa* (Hooker) Barneby

var. *culminis* Jepson, Fl. Calif. 2: 381. 1936.
Type: Cottonwood Creek, White Mts., Mono Co., California, V. Duran 1650, 29 June 1926; holotype UC!
= *O. deflexa* var. *sericea* Torrey & Gray

var. *deflexa*
Distribution: Colorado, Utah, and reported (Barneby 1952) less commonly elsewhere in North America; Asia.
As interpreted by me and by Barneby (1952), plants similar to the typical Siberian material of the species occur disjunctly in America, mainly in the mountains of Colorado and Utah. The combination of racemes with 10 to 20 large flowers on plants that are mainly acaulescent or short caulescent forms a distinctive morphology. They differ from var. *foliolosa* in about the same manner that that variety differs from var. *sericea*.

var. *dezhnevii* Jurtsev, Bot. Journ. 57: 6, 647. 1972.
Type: ?
= *O. deflexa* var. *foliolosa* (Hooker) Barneby
The placement of this plant with var. *foliolosa* is based on examination of authentic material of the proposed entity in the herbarium at BRY. The specimens examined from western Alaska are somewhat more apparently black hairy than materials from farther east. Otherwise they seem to fit within the broad concept of var. *foliolosa*.

ssp. *dezhnevii* (Jurtsev) Jurtsev, Arctic Fl. S.S.S.R. 9: 79. 1986.
Basionym: *O. deflexa* var. *dezhnevii* Jurtsev

var. *foliolosa* (Hooker) Barneby, Leafl. W. Bot. 6: 111. 1951.
Basionym: *Astragalus deflexus* Pallas
Distribution: Rocky Mountains, from Alaska to Nevada and Wyoming; also on arctic and subarctic shores of Mackenzie, Ungava Peninsula, Baffin Island, Labrador, Newfoundland, and Gaspe Peninsula.

This is the most showy of the two common phases of the species in North America. The flowers are typically brightly colored in compact to subcompact racemes with up to 10 flowers. Sometimes there are more flowers in rather lax racemes, but the racemes seldom surpass 10 cm long even in fruit. The herbage is typically sparingly pilose and green in aspect, and both caulescent and acaulescent phases occur. Some of the variation, especially portions of that regarded as var. *capitata* Boivin, is geographically correlated. Further segregation, however, seems unnecessary. Transitional specimens to var. *sericea* are known.

var. *parviflora* Boivin, Svensk Bot. Tidskr. 56: 498. 1962.
Type: Alberta, Ft. Smith, 1 mi SW, black sandy soil in Populus spp., Salix spp., Picea glauca woods along trail, W. J. Cody & C. C. Loan 4496, 17 July 1950; holotype DAO!; isotype RM!
= *O. deflexa* (Pallas) de Candolle var. *sericea* Torrey & Gray

ssp. *retrorsa* (Fernald) Love & Love, Taxon 31: 347. 1982.
Basionym: *O. retrorsa* Fernald
= *O. deflexa* var. *sericea* Torrey & Gray

β [var.] *sericea* Torrey & Gray, Fl. N. Amer. 1: 242. 1838.
Type: "Rocky Mountains near streams" [Wyoming or Idaho], T. Nuttall s.n., 1834; holotype NY!
Distribution: Alaska, Yukon, N.W.T., British Columbia, Alberta, Manitoba, Washington, California, Idaho, Montana, New Mexico, Oregon, Utah, and Wyoming.
This is the common phase of *O. deflexa* south of the Arctic. The variety is highly variable, especially in size and aspect of the flowers. The small-flowered phase of the northern Rockies was proposed as var. *parviflora* Boivin. Flowers of some of the variants appear not to open, as if they are cleistogamous. Further work is indicated on this group.

Oxytropis dispar (A. Nelson) K. Schumann, Just's Bot. Jahresb. 27: 496. 1901.
Basionym: *Aragallus dispar* A. Nelson
= *O. campestris* (L.) de Candolle var. *dispar* (A. Nelson) Barneby

Oxytropis falcata (Greene) A. Nelson, Univ. Wyo. Pub. Bot. 1: 118. 1926.
Basionym: *Aragallus falcatus* Greene
= *O. lambertii* var. *lambertii*

Oxytropis foliolosa Hooker, Fl. Bor.-Amer. 1: 146. 1831.
Type: "Carlton House to the Rocky Mountains, in lat. 54°" [Alberta], collector not noted, probably T. Drummond; holotype K; isotype NY!
= *O. deflexa* var. *foliolosa* (Hooker) Barneby

Oxytropis gaspensis Fernald & Kelsey, Rhodora 30: 123. 1928.
Type: Quebec, Gaspe County, dry talus of slaty cliffs, northern face of Mt. St. Pierre, at mouth of Riviere a Pierre, M. L. Fernald & L. B. Smith 25874, 14 August 1923; holotype GH!; isotypes MO!, CAS!, NY!
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

Oxytropis glaberrima Hulten, Bot. Tidskr. 5: 124. 1954.
Type: Alaska, Kurupa Valley, 7 mi N of Kurupa Lake, A. R. Hodgdon 8060, 25 June 1952; holotype S!
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

Oxytropis glabrata (Hooker) A. Nelson, Univ. Wyo. Pub. Bot. 1: 117. 1926
Basionym: *O. campestris* ε *glabrata* Hooker.
= *O. maydelliana* Trautvetter

Oxytropis glutinosa Porsild, Bull. Nat. Mus. Canad. 121: 240. 1951.
Type: Yukon, Canol Rd.: Mile 132. Lower Lapie Crossing, dry shaly slopes of mountain west of road, A. E. Porsild & A. J. Breitung 9730, 20 June 1944; holotype CAN; isotypes GH!, ISC!, S!, NY!, US!
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

Oxytropis gorodkovii Jurtsev, Bot. Journ. 53: 11. 1968 (nom. nov. pro *Astragalus pygmaeus* Pallas; *O. pygmaea* [Pallas] Fernald).
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

Oxytropis gracilis (A. Nelson) K. Schumann, Just's Bot. Jahresb. 24: 496. 1901.
Basionym: *Aragallus gracilis* A. Nelson
= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

Oxytropis hallii Bunge, Gen. Oxytropis, 162. 1874.
Type: Rocky Mts., Lat. 39°–41°, E. Hall & H. Harbour 143 (in part), 1862; isotypes GH!, NY (in packet)!, US!
= *O. podocarpa* A. Gray

Oxytropis hookeriana Nuttall ex Torrey & Gray, Fl. N. Amer., 340. 1838
Type: "*O. hookeri*. *O. lambertii* Hook. Platte Plains. T. Nuttall"; holotype BM.
= *O. lambertii* var. *lambertii*

Oxytropis huddlesonii Porsild, Bull. Nat. Mus. Canad. 121: 242. pl. 17, fig. 5. 1951.
Type: Yukon, Golden Horn Mountain, south of Whitehorse, in lichen heath above timberline, elevation 5,800 feet, C. W. Huddleson s.n. 1944; holotype CAN!
Distribution: S and E Alaska, S Yukon, and N British Columbia; endemic.
The presence of unilocular, glabrous or sparingly strigose pods distinguishes this entity from *O. nigrescens*, its apparent close ally in boreal northwestern North America.

Oxytropis hudsonica (Greene) Fernald, Rhodora 30: 142, pl. 172. 1928.
Basionym: *Aragallus hudsonicus* Greene
= *O. borealis* de Candolle var. *hudsonica* (Greene) Welsh

Oxytropis hyperborea Porsild, Sargentia 4: 53. 1943.
Type: N.W.T., Mackenzie R. Delta, E branch, 68°55′N, A. E. Porsild 7033, 21 July 1934; holotype CAN; isotype GH!, S!, US!
= *Oxytropis campestris* (L.) de Candolle var. *varians* (Rydberg) Barneby

Oxytropis inflata (Hooker) Steffen, Beih. Bot. Centralbl. 58B: 162. 1938.
Basionym: *O. arctica* δ *inflata* Hooker
= *O. podocarpa* A. Gray

Oxytropis involuta **(A. Nelson) K. Schumann,** Just's Bot. Jahresb. 27: 496. 1901.

Basionym: *Aragallus involutus* A. Nelson

= *Oxytropis lambertii* Pursh var. *lambertii*

Oxytropis ixodes **Butters & Abbe,** Rhodora 45: 2, tab. 745, figs. 1–6. 1943.

Type: Minnesota, slate cliffs on north side of a high hill 1/2 mi. west of the outlet of South Fowl Lake, Cook County, F. K. Butters, E. C. Abbe, & G. W. Burns 611, 27 June 1940; holotype MIN; isotype GH!, NY!, PH!, US!, UC!, DAO!

= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. *ecaudata* **Butters & Abbe,** Rhodora 45: 4. 1943.

Type: Ontario, slate cliffs east of North Fowl Lake, Thunder Bay District, F. K. Butters, E. C. Abbe, & G. W. Burns 682, 1 July 1940; holotype MIN; isotype GH!

= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

Oxytropis johannensis **(Fernald) Fernald,** Rhodora 30: 1435, pl. 173. 1928.

Basionym: *O. campestris* (L.) de Candolle var. *johannensis* Fernald

f. *bicensis* **Victorin & Rousseau,** Cont. Inst. Bot. Univ. Montreal 36: 32. 1940.

Type: Quebec, Rimoufski Co., St. Fabien, Montagne du Bic, J. Rousseau 50297, 15 July 1986; holotype ?; isotype DAO!

= *O. campestris* (L.) de Candolle var. *johannensis* Fernald

Oxytropis jonesii **Barneby,** Proc. Calif. Acad. IV, 27: 215. 1952.

Type: Utah, pink calcareous gravel benches, Red Canyon, Garfield County, alt. 7150 ft., 1947, H. D. Ripley & R. C. Barneby 8550, 7 June 1947; holotype CAS!, isotypes GH!, NY!, RM!

=*O. oreophila* var. *jonesii* (Barneby) Barneby

Oxytropis jordallii **Porsild,** Canad. Field-Nat. 65: 77, tab. 1. 1951.

Type: Alaska, Old John Lake, L. H. Jordal 3580, 1950; holotype CAN; isotypes US!, S!

= *O. campestris* (L.) de Candolle var. *jordalii* (Porsild) Welsh

ssp. *davisii* **(Welsh) Elisens & Packer,** Canad. J. Bot. 58: 1830. 1980.

Basionym: *O. campestris* (L.) de Candolle var. *davisii* Welsh

= *O. campestris* (L.) de Candolle var. *davisii* Welsh

Oxytropis kobukensis **Welsh,** Iowa State J. Sci. 41: 286. 1967.

Type: Alaska, sand dunes, Kobuk River, across from the mouth of the Hunt River, R. D. Hamilton s.n., 1938; holotype BRY!

Distribution: Sand dunes, Kobuk River, W Alaska; endemic.

The enlarged, purplish stipules on elongate caudex branches are characteristic of this pink-purple flowered plant of dunes in western Alaska. The relationship of this entity likely lies with Siberian species. Jurtsev points to *O. ochotensis* Bunge as having possible relationship. The few specimens of that taxon examined seem to be smaller in all parts and to have chestnut colored stipules rather than the merely purplish suffused ones of *O. kobukensis*.

Oxytropis kokrinensis **Porsild,** Rhodora 41: 251, tab. 553. 1939.

Type: Kokrines Mountains, north side of divide towards Melozitna River, 65°20′N, 154°30′W, alpine slopes 2000–4000 ft, A. E. & R. T. Porsild 762, 1926; holotype CAN!, fragment S!

Distribution: Ridge tops in the Kokrines Mountains and western Brooks Range, Alaska; endemic.

This species is evidently allied to *O. podocarpa* by its inflated, stipitate pods. It is easily distinguished from that entity by its purplish stipules.

Oxytropis koyukukensis **Porsild,** Canad. Field-Nat. 65: 78. 1951.

Type: Alaska, Wiseman, L. H. Jordal 1763, 15 June 1944; holotype CAN!; isotype US!, ISC!

= *O. arctica* R. Brown var. *koyukukensis* (Porsild) Welsh

Oxytropis lagopus **Nuttall,** J. Acad. Philad. 7: 17. 1834.

Type: Sources of the Missouri, N. B. Wyeth s.n., 1833; holotype PH!; isotype NY!

var. *atropurpurea* **(Rydberg) Barneby,** Leafl. W. Bot. 5: 111. 1951.

Basionym: *Aragallus atropurpureus* Rydberg, Bull. Torrey Bot. Club 34: 424. 1907.

Distribution: SE Montana, Wyoming, and South Dakota.

var. *conjugans* **Barneby,** Proc. Calif. Acad. IV, 27: 227. 1952.

Type: Vicinity of Helena, Montana, E. O. Wooton s.n., 1921; holotype US!; isotype NY!

Distribution: W Montana and S Alberta; endemic.

var. *lagopus*

Distribution: N and E Idaho, W Montana, and N Wyoming.

Oxytropis lambertii **Pursh,** Fl. Amer. Sept., 740. 1814.

Type: "On the Missouri, on the bluffs from the Maha village to the Poncars, Louisiana [NE Nebraska or adjacent South Dakota or Iowa], Bradbury s.n., 1811; holotype PH!

β Hooker, Fl. Bor.-Amer. 1: 107. 1834.

Type: Oxytropis lambertii β. Dr. Hooker; isotype NY!

= *O. campestris* (L.) de Candolle var. *davisii* Welsh

γ Torrey & Gray, Fl. N. Amer. 1: 339. 1838.

Type: ?

= *O. lambertii* var. *lambertii*

δ ? Torrey & Gray, Fl. N. Amer. 1: 338. 1838.

Type: Quebec, near Quebec, Mrs. Percival s.n.; holotype NY!

= *O. campestris* (L.) de Candolle var. *johannensis* Fernald

var. *articulata* **(Greene) Barneby,** Leafl. W. Bot. 5: 111. 1951.

Basionym: *Aragallus articulatus* Greene

Distribution: Kansas (Meade Co.), Oklahoma, and Texas.

This plant of the southern prairies and plains is distinguished by its short calyx teeth, large flowers, and shortly exserted or included pods.

ssp. ***bigelovii*** **(A. Gray) W. A. Weber,** Phytologia 51: 374. 1982.
Basionym: *O. lambertii* var. *bigelovii* A. Gray
= *O. lambertii* var. *bigelovii* A. Gray

var. *bigelovii* A. Gray, Proc. Amer. Acad. 20: 7. 1884.
Type: Rocky hillsides, upper Canadian [Guadalupe or San Miguel County, New Mexico], J. M. Bigelow s.n., Sept. 21, 1853; holotype GH!; isotype US!
Distribution: SE Wyoming, Colorado, New Mexico, Arizona, and Utah.
This plant typically has large flowers and short to elongate calyx teeth and pods. It is mainly a montane or intermontane variety, which abuts with var. *lambertii* in Colorado and Wyoming. Materials of var. *bigelovii* from the canyonlands of Utah and adjacent Arizona have malpighian hairs with very short attachment. Furthermore, the plants tend to be tall, with features of scape, inflorescence, and leaflets attenuated. The leaflets further tend to disarticulate from the rachis readily. Northward from the canyonlands of Kane and San Juan counties, Utah, the attenuation of parts fails, even though the short branch of the malpighian hair persists. There does not seem to be sufficient correlation of morphological features to warrant taxonomic status for these plants that are obviously in transition.

f. *canadensis* Gandoger, Bull. Soc. Bot. France 48: xvi. 1901.
Type: Southern Manitoba in the valley of the Souris River, Portage-la-Prairie, MacMorine s.n., Aug. 1897; syntype DAO!
= *O. campestris* (L.) de Candolle var. *gracilis*

var. *lambertii*
Distribution: British Columbia, Saskatchewan, Manitoba, Montana, North Dakota, Minnesota, South Dakota, Wyoming, Nebraska, Iowa, Kansas, Missouri, and Wyoming.
The coincidence of long calyx teeth, small flowers, and elongate pods is diagnostic for this variety of the central and northern prairies and plains.

var. *lilacina* Cockerell, W. Amer. Sci. 5: 11. 1888, nomen.
= *O. sericea* Nuttall var. *sericea*

f. *mixta* Gandoger, Bull. Soc. Bot. France 48: xvii. 1901
Type: Minnesota, Montevideo, L. Moyer s.n., 1909; Wyoming, head of Pole Creek, A. Nelson 1320, 27 June 1895; syntypes NY!
= *O. lambertii* var. *lambertii*

var. *ochroleuca* A. Nelson, Bull. Wyo. Exper. Sta. 28: 98. 1896.
Type: Wyoming, Pole Creek, Albany County, A. Nelson 119, 2 June 1894; holotype RM!; isotype NY!, photo BRY! Nelson named this plant three times, in 1896 as *O. lambertii* var. *ochroleuca*, in 1899 as *Aragallus albiflorus*, and in 1900 as *Aragallus saximontanus*. All are typified on the same collection.
= *O. sericea* Nuttall var. *sericea*

var. *sericea* (Nuttall) A. Nelson, Erythea 7: 62. 1899.
Basionym: *O. sericea* Nuttall
= *O. sericea* Nuttall var. *sericea*

Oxytropis leucantha **(Pallas) Persoon,** Syn. 2: 331. 1807.
Basionym: *Astragalus leucanthus* Pallas
Note: All combinations cited are synonyms of phases of *O. borealis* de Candolle—*O. leucantha* (Pallas) Persoon belongs to *O. campestris* sens. lat., but Jurtsev (1986) regards it as a separate species allied to *O. sordida* (Willdenow) Persoon.

var. *depressa* (Rydberg) Boivin, Naturaliste Canad. 94: 77. 1967.
Basionym: *Aragallus viscidulus* var. *depressus* Rydberg
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. *hudsonica* f. *galactantha* Boivin, Naturaliste Canad. 94: 76. 1967.
Type: Canada: Franklin District, Melville Peninsula, Repulse Bay, along Nauja River, P. F. Bruggeman 52, 27 July 1950; holotype DAO!
= *O. borealis* de Candolle var. *hudsonica* (Greene) Welsh

var. *gaspensis* (Fernald & Kelsey) Boivin, Naturaliste Canad. 94: 76. 1967
Basionym: *Oxytropis gaspensis* Fernald & Kelsey
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. *hudsonica* (Greene) Boivin, Naturaliste Canad. 94: 76. 1967.
Basionym: *Aragallus hudsonicus* Greene
= *O. borealis* de Candolle var. *hudsonica* (Greene) Welsh

var. *ixodes* (Butters & Abbe) Boivin, Naturaliste Canad. 94: 76. 1967.
Basionym: *Oxytropis ixodes* Butters & Abbe
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. *leuchippiana* Boivin, Naturaliste Canad. 94: 76. 1967.
Type: Yukon: Whitehorse, airport area, steep slope, flowers varying in colour from yellow to purple, abundant, J. M. Gillett & J. A. Calder 3181, 4 June 1949; lectotype here selected DAO!; isolectotype CAS!
= *O. borealis* de Candolle var. *hudsonica* (Greene) Welsh

var. *magnifica* Boivin, Naturaliste Canad. 94: 77. 1967.
Type: Alberta, High River, J. Fletcher 457 1/2, 27 June 1902; holotype DAO!
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. *viscida* (Nuttall) Boivin, Naturaliste Canad. 94: 77. 1967.
Basionym: *O. viscida* Nuttall
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

Oxytropis lunelliana **A. Nelson,** Univ. Wyo. Pub. Bot. 1: 117. 1926, nom. nov.
Basionym: *Aragallus collinus* A. Nelson
= *Oxytropis sericea* Nuttall var. *spicata* (Hooker) Barneby

Oxytropis luteola **(Greene) Piper & Beattie,** Fl. N.-W. Coast, 334. 1915.
Basionym: *Aragallus luteolus* Greene
= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

Oxytropis macounii **(Greene) Dayton,** Proc. Biol. Soc. Wash. 40: 120. 1927.

Basionym: *Aragallus macounii* Greene

= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Oxytropis maydelliana* Trautvetter,** Act. Hort. Petrop. 6: 16. 1879.

Type: ". . . in tractu fluvium Anadyr inter et latus meridionale montium jugi a fluvio hoc septentrionem versus siti" [Chukchi, from the basin of the Anadyr and its northern tributaries], Baron G. von Maydell s.n., 1869; holotype LE?

Distribution: Alaska, Yukon, N British Columbia, N.W.T., E to Hudson Bay and Baffin Island; Chukotsk and Kamchatica.

The yellowish flowers and reddish brown stipules easily characterize this arctic species.

ssp. *melanocephala* (Hooker) Porsild, Nat. Mus. Canada Bull. 216: 47. 1966.

Basionym: *O. campestris* (L.) de Candolle var. *melanocephala* Hooker

= *O. maydelliana* Trautvetter

***Oxytropis mazama* St. John,** Proc. Biol. Soc. Wash. 41: 101. 1928.

Type: Washington, Goat Mts., Pierce County, O. D. Allen 245, 6 July, 30 September 1896; holotype WTC; isotype NY!, US!, CAS!, UC!

= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Oxytropis mertensiana* Turczaninow,** Bull. Soc. Nat. Mosc., 1840:68. 1840.

Type: "ad sinum Sancti Laurentii," Dr. Mertens; holotype LE.

Distribution: Disjunct in E, N, W Alaska, and N Yukon; arctic Siberia and west to ca 60° E longitude (Jurtsev 1986).

This plant is easily distinguished by its simple primary and trifoliolate secondary leaves in conjunction with few-flowered, densely black-villous inflorescences.

***Oxytropis minor* (A. Gray) Cockerell,** Torreya 18: 180. 1918.

Basionym: *Oxytropis multiceps* var. *minor* A. Gray

= *O. multiceps* Torrey & Gray

***Oxytropis mollis* Nuttall ex A. Gray,** Proc. Amer. Acad. 6: 235. 1864, synonym.

= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

***Oxytropis monticola* A. Gray,** Proc. Amer. Acad. 20: 6. 1884.

Type: Montana, Valley of Jocko River, Lake County, W. M. Canby 91, 18 July 1883; lectotype (Barneby, Proc. Calif. Acad. Sci. IV, 27: 257. 1952) GH!

= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

This name is lectotypified by Barneby (1952), who selected the type from among a series of specimens cited by Dr. Gray. The syntypes were a mixed lot, with C. C. Parry 87 being a putative hybrid between *O. campestris* var. *gracilis* and *O. borealis* var. *viscida*, Jenney s.n. 1875 belonging to *O. campestris* var. *dispar*, and Lyall s.n. 1862 belonging to *O. campestris* var. *cusickii*. The lectotypification was reviewed by Elisens and Packer (1982).

ssp. *dispar* (A. Nelson) Elisens & Packer, Canad. J. Bot. 58: 1826. 1980.

Basionym: *Aragallus dispar* A. Nelson

= *O. campestris* (L.) de Candolle var. *dispar* (A. Nelson) Barneby

***Oxytropis multiceps* Torrey & Gray,** Fl. N. Amer. 1: 341. 1838.

Type: "Summit of lofty hills in the Rocky Mountain range, towards Lewis's River [S Wyoming], Rocky Mts.," T. Nuttall s.n., 1834; holotype GH!; isotypes NY!, PH!

Distribution: Colorado, NE Utah, S Wyoming, and W Nebraska.

The accrescent calyces, broad bracts, and few flowers are characteristic for the species, which stands alone in the genus in North America in its morphology.

var. *minor* A. Gray, Proc. Amer. Acad. 20: 2. 1884.

Type: Clear Creek County, Colorado, C. C. Parry 991, 1861; lectotype (here designated by Welsh, cf. Barneby, Proc. Calif. Acad. Sci. IV, 27: 220. 1952) GH!; isolectotype NY!

= *O. multiceps* Torrey & Gray

***Oxytropis nana* Nuttall ex Torrey & Gray,** Fl. N. Amer. 1: 340. 1838.

Type: Plains of the Platte in the Rocky Mountain Range [Wyoming], T. Nuttall s.n. 1834; holotype PH!; isotype NY!

Distribution: Drainage of the North Platte and Cheyenne rivers, westward to the Wind River Mountains, Albany, Carbon, Converse, Fremont, Natrona, Platte, and Sweetwater counties, Wyoming; endemic.

This is a beautiful species of clays, shales, and gravelly bluffs and ridge tops endemic to Wyoming. Barneby (1952) postulated that it might have arisen through hybridization of *O. sericea* and *O. multiceps*, a very likely supposition. Flower colors are variable in a given population from pale pinks through lavender and purple, and white-flowered populations are known. A contribution from *O. lambertii* is also suggested by the presence of incipiently malpighian hairs in some specimens. The relationship to segregates of *O. besseyi* seems tenuous at best. The relegation of *O. nana* to that species might require a realignment of other taxa as well, including combination of *lambertii*, *sericea*, *campestris*, and even *multiceps*. Such a proposal is, of course, absurd. Taxonomy must be both practical and reflect biological reality.

var. *argophylla* (Rydberg) Isely, Syst. Bot. 8: 425. 1983.

Basionym: *Aragallus argophyllus* Rydberg

= *O. besseyi* (Rydberg) Blankinship var. *argophylla* (Rydberg) Isely

var. *besseyi* (Rydberg) Isely, Syst. Bot. 8: 425. 1983.

Basionym: *Aragallus besseyi* Rydberg

= *O. besseyi* (Rydberg) Blankinship var. *besseyi*

var. *fallax* (Barneby) Isely, Syst. Bot. 8: 425. 1983.

Basionym: *O. besseyi* (Rydberg) Blankinship var. *fallax* Barneby

var. *obnapiformis* (C. L. Porter) Isely, Syst. Bot. 8: 425. 1983.

Basionym: *O. obnapiformis* C. L. Porter

var. *salmonensis* (Barneby) Isely, Syst. Bot. 8: 425. 1983.
Basionym: *O. besseyi* (Rydberg) Blankinship var. *salmonensis* Barneby

var. *ventosa* (Greene) Isely, Syst. Bot. 8: 425. 1983.
Basionym: *Aragallus ventosa* Greene

***Oxytropis nigrescens* (Pallas) Fischer ex de Candolle,** Prodr. 2: 278. 1825.

ssp. *arctobia* (Bunge) Hulten, Ark. Bot. (n.s.) 7: 80. 1968.
Basionym: *O. arctobia* Bunge
= *O. nigrescens* (Pallas) Fischer var. *uniflora* (Hooker) Barneby

var. *arctobia* (Bunge) A. Gray, Proc. Amer. Acad. 20: 3. 1884
Basionym: *O. arctobia* Bunge
= *O. nigrescens* (Pallas) Fischer var. *uniflora* (Hooker) Barneby

ssp. *bryophila* (Greene) Hulten, Fl. Alaska & Yukon, 1102, map 833. 1947.
Basionym: *Aragallus bryophilus* Greene, Proc. Biol. Soc. Wash. 18: 17. 1905.
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

var. *bryophila* (Greene) Lepage, Amer. Midl. Nat. 46: 758. 1952
Basionym: *Aragallus bryophilus* Greene
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

var. *bryophila* f. *albida* Lepage, Amer. Midl. Nat. 46: 758. 1952.
Type: Alaska, Kodiak, Old Woman Mt., Lepage 25089, 24 June 1949; holotype ?; isotype DAO!, RIM!, fragment BRY!
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

var. *genuina* Kjellman, Vega-Exped. Vetensk. Arb., 16. 1883, nomen.
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

var. *lonchopoda* Barneby, Leafl. W. Bot. 10: 23. 1963.
Type: Yukon, Cathedral Rocks, Ogilvie Range, J. A. Calder & J. M. Gillett 26013A, 29 June 1960; holotype DAO!; isotype NY!
Distribution: Ogilvie Mts., Yukon; endemic.

The variety rests almost solely upon the pods being definitely stipitate. There is considerable variation in stipe length through the range of *O. nigrescens* apart from the phase segregated as var. *lonchopoda*. The localization of an elongated stipe in plants from the Ogilvie Mts. might prove ultimately to represent a mere continuum and lack value in designation of a taxon. Plants from there in vegetative condition are essentially like those of phases of *O. nigrescens* from elsewhere. The elongate stipe and slightly inflated pods are reminescent of *O. podocarpa*, but the leaflets are as in var. *nigrescens*.

var. *nigrescens*
Distribution: Amphiberingian, coastal Yukon to Bering Strait, south to Kodiak, and in interior Yukon and Alaska, N.W.T. (Mackenzie Mts.), and British Columbia; Siberia and Kamchatka.

This is a highly variable taxon with green and silvery, loose and compact, villous to strigose or even glabrous plants growing intermingled. And, it is with the often mixed variants that infraspecific segregation has been attempted. The synonymy is long, indicating the diversity of form but not necessarily the presence of several taxa within the complex morphology of the species.

ssp. *pygmaea* (Pallas) Hulten, Fl. Alaska & Yukon, 1102. 1947
Basionym: *Astragalus pygmaeus* Pallas
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

var. *pygmaea* (Pallas) Chamisso, Linnaea 6: 546. 1831.
Basionym: *Astragalus pygmaeus* Pallas
= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

var. *uniflora* (Hooker) Barneby, Proc. Calif. Acad. IV, 27: 209. 1952.
Basionym: *O. arctica* β *uniflora* Hooker
Distribution: Islands of the Canadian Arctic Archipelago and along the arctic coast from Mackenzie Delta E to Baffin Island and Hudson Bay, less commonly in interior sites in Yukon.

This plant, as interpreted by me, is an American (more precisely a Canadian) endemic, but there are plants from the Chukotsk that match them closely (see *O. gorodkovii* Jurtsev, a new name for *O. pygmaea*, a phase of var. *nigrescens*). The Siberian materials seem to represent mere ecological variants within an expanded var. *nigrescens*, however.

***Oxytropis obnapiformis* C. L. Porter,** Madrono 9: 133, fig. 1947.
Type: Colorado, in the sand hills 8–9 mi W of Maybell, Moffat County, 5,900 ft., C. L. Porter 3864, 19 June 1946; holotype RM!; isotypes GH!, RSA, US!
= *O. besseyi* (Rydberg) Blankinship var. *obnapiformis* (C. L. Porter) Welsh

***Oxytropis okanoganea* St. John,** Proc. Biol. Soc. Wash. 41: 102. 1928.
Type: Washington, n.w. of Riverside, Okanogan County, H. St. John 7728; holotype WTC.
= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Oxytropis olympica* St. John,** Proc. Biol. Soc. Wash. 41: 103. 1928.
Type: Washington, Olympic Mts., Jefferson County, B. Flett 134, 24 July 1897; holotype WTC; isotype US!, photo BRY!
= *O. campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

***Oxytropis oreophila* A. Gray,** Proc. Amer. Acad. 20: 3. 1884.
Type: Utah, Aquarius Plateau, 10,500 ft., Garfield County, L. F. Ward 541, 9 August 1875; lectotype (here designated by Welsh, cf. Barneby, Proc. Calif. Acad. Sci. IV, 27: 214. 1952) GH!, isolectotype NY!

var. *jonesii* (Barneby) Barneby, Intermountain Fl. 3B: 183. 1989.
Basionym: *O. jonesii* Barneby
Distribution: Uinta Basin, Wasatch Plateau, and Paunsaugunt and Markagunt plateaus, Utah; endemic.

This is a caespitose, mat- or mound-forming plant, of moderate elevations in mountain brush or ponderosa pine zones. Its compact growth, large flowers, and short peduncles are characteristic for the variety. It is more or less transitional with the next variety.

var. *juniperina* Welsh, Great Basin Nat. 38: 339. 1978.

Type: Utah, ca 1 mi E of Bicknell, Wayne County, S. L. Welsh & G. Moore 13828, 1976; holotype BRY!; isotype NY!

Distribution: Nevada and Utah; endemic.

This ia a caespitose, mat- or mound-forming plant, of low-elevation, xeric sites. The compact growth, smallish flowers, and short peduncles are characteristic for the variety.

var. *oreophila*

Distribution: Arizona, California, Nevada, and Utah.

This is the taller, more robust phase of the species with elongate scapes bearing clustered, bladdery-inflated pods, more typical of high elevations where it often grows intermingled with *O. parryi*.

***Oxytropis parryi* A. Gray**, Proc. Amer. Acad. 20: 4. 1884.

Type: "Rocky Mountains of northern New Mexico and Colorado, near the limit of trees" [Sangre de Cristo Pass, Taos Co., N.M.], C. C. Parry 41, 1867; lectotype (here designated by Welsh, cf. Barneby, Proc. Calif. Acad. Sci. IV, 27: 218. 1952) GH!. Rocky Mountains, E. Hall & H. Harbour; cotypes GH!, NY!

Distribution: Montana (?), Idaho, Wyoming, California, Nevada, Utah, Colorado, and New Mexico.

***Oxytropis patens* (Rydberg) A. Nelson**, Univ. Wyo. Pub. Bot. 1: 114. 1926.

Basionym: *Aragallus patens* Rydberg

= *Oxytropis lambertii* Pursh var. *bigelovii* A. Gray

***Oxytropis paysoniana* A. Nelson**, Univ. Wyo. Pub. Bot. 1: 119. 1926.

Type: Wyoming, Piney Mt., 25 miles west of Big Piney, Sublette County, E. & L. Payson 2700, July 12, 1922; holotype RM!; isotypes NY!, US!

= *O. campestris* (L.) de Candolle var. *cusickii* (Greenman) Barneby

***Oxytropis pinetorum* (A. Heller) K. Schumann**, Just's Bot. Jahresb. 27: 496. 1901.

Basionym: *Aragallus pinetorum* A. Heller

= *O. sericea* Nuttall var. *sericea*

***Oxytropis plattensis* Nuttall ex Torrey & Gray**, Fl. N. Amer. 1: 340. 1838.

Type: Platte Plains, Nuttall s.n.; isotype NY!

= *O. lambertii* var. *lambertii*

***Oxytropis podocarpa* A. Gray**, Proc. Amer. Acad. 6: 234. 1864.

Type: Labrador (Schweinitz) and Alberta (Bourgeau); cotypes GH! The specimens are cotypical, both having been used by Gray in characterization of the species.

Distribution: Rocky alpine ridges and coastal shores, in Colorado, Wyoming, Montana, Alberta, N.W.T., Ungava Peninsula, Labrador, and Baffin Island.

The bladdery-inflated stipitate pods are characteristic of this and few other species of oxytrope. The folded, falcate leaflets are useful in distinguishing this from closely related mat- or mound-forming species, such as *O. nigrescens*, in vegetative condition.

var. *inflata* (Hooker) Boivin, Naturaliste Canad. 94: 78. 1967.

Basionym: *O. arctica* δ *inflata* Hooker

= *O. podocarpa* A. Gray

***Oxytropis pygmaea* (Pallas) Fernald**, Rhodora 30: 153. 1928.

Basionym: *Astragalus pygmaeus* Pallas

= *Oxytropis nigrescens* (Pallas) Fischer var. *nigrescens*

***Oxytropis retrorsa* Fernald**, Rhodora 30: 140. 1928.

Type: Colorado, vicinity of Como [Park Co.], South Park, C. S. Crandall & J. S. Cowen 152, August 3, 1895; holotype GH!; isotype NY!

= *O. deflexa* var. *sericea* Torr. & Gray

var. *sericea* (Torrey & Gray) Fernald, Rhodora 30: 140. 1928.

O. retrorsa ssp. *sericea* (Torrey & Gray) Love & Love, Taxon 31: 347. 1982.

= *O. deflexa* var. *sericea* Torrey & Gray

***Oxytropis richardsonii* (Hooker) K. Schumann**, Just's Bot. Jahresb. 27: 496. 1901.

Basionym: *O. splendens* β *richardsonii* Hooker

= *O. splendens* Douglas

***Oxytropis riparia* Litvinov**, Sched. Herb. Fl. Ross. 6: 98. 1908.

Type: Russian Turkestan, from Farab (on the Amu Darya); holotype LE.

Distribution: Idaho, Montana, North Dakota, and Wyoming; introduced from central Asia.

This is a coarse perennial herb with the general aspect of *O. deflexa* (Pallas) de Candolle. It grows in riparian habitats where it is grazed by wildlife, especially by sage hens. The species is expected to spread in suitable habitats through much of the American West.

***Oxytropis roaldii* Ostenfeld**, Vasc. Pl. Arctic N. Amer. Gjoa Exped., 54, pl. 3, fig. 16. 1910.

Type: Iter arcticus Roald Amundsen (Gjoa-Expedition) 1903–1906. America Arct., Herschell Island, Lat N 69°35′ Long. W 138°50′, 13 July 1906, A. H. Lindstrom s.n.; isotype NY!

= *O. campestris* (L.) de Candolle var. *roaldii* (Ostenfeld) Welsh

***Oxytropis rydbergii* A. Nelson**, Univ. Wyo. Pub. Bot. 1: 117. 1926.

nom. nov. pro *Aragallus alpicola* Rydberg

= *O. campestris* (L.) de Candolle var. *cusickii* (Greenman) Barneby

***Oxytropis saximontana* (A. Nelson) A. Nelson**, Univ. Wyo. Pub. Bot. 1: 113. 1926.

Basionym: *Aragallus saximontanus* A. Nelson, nom. nov. *Oxytropis lambertii* Pursh var. *ochroleuca* A. Nelson

= *Oxytropis sericea* Nuttall var. *sericea*

***Oxytropis scammaniana* Hulten**, Ark. Bot. 33B: 4, figs. 2, 3 (map). 1947.

Type: Alaska, Eagle Summit, near Steese Highway 109 miles north of Fairbanks, elevation 3880 feet,

E. Scamman 806, 7–11 July 1937; holotype S!; isotype GH!; photo BRY!

Distribution: Alaska, Yukon, and N.W.T. (Mackenzie Mts.); endemic.

This plant is similar to *O. mertensiana*, possibly its nearest ally in North America, in both inflorescence and pod aspect and structure.

***Oxytropis sericea* Nuttall ex Torrey & Gray**, Fl. N. Amer. 1: 39. 1838.

Type: Rocky Mountains towards the sources of the Oregon [S Wyoming], T. Nuttall s.n., 1834; holotype NY!

var. *sericea*

Distribution: Montana, Wyoming, South Dakota, Nebraska, Idaho, Oregon, Nevada, Utah, Colorado, Kansas, New Mexico, and Oklahoma.

This variety forms hybrids with *O. lambertii* at points where the two entities come in contact. Especially impressive hybrid populations occur along the western Great Plains and in the Rocky Mountain foothills. The great swarms of hybrids, back crosses, and derivatives at Nederland, Colorado, are especially distinctive, with floral colors and sizes not readily evident in either of the parental types. There are indications, also, of transitional material between this variety and phases of *O. besseyi*.

var. *spicata* (Hooker) Barneby, Leafl. W. Bot. 5: 111. 1951.

Basionym: *O. campestris* (L.) de Candolle δ *spicata* Hooker

Distribution: Yukon, British Columbia, Alberta, Saskatchewan, Manitoba, Montana, Idaho, and Wyoming.

Members of this variety are characterized by their ochroleucous flowers with immaculate keels. In general aspect they simulate the partially sympatric *O. campestris* var. *gracilis*, from which they may be distinguished on the basis of the smaller number of leaflets and generally larger flowers. Alpine phases of *O. campestris* var. *cusickii* approach both flower size and color of var. *sericea*. Mainly var. *sericea* is not a plant of the highlands where that variety grows, but the similarities should not be discounted. Apparent hybrids are known between this and *O. campestris* var. *davisii* in northeastern British Columbia.

***Oxytropis sheldonensis* Porsild,** Bull. Nat. Mus. Canad. 121: 246. 1951.

Type: Yukon, Canol Rd.: South and east slopes of Mt. Sheldon, steep ravines and ledges opposite mile 222, A. E. Porsild & A. J. Breitung 11750, 11 August 1944; holotype CAN!; isotypes GH!, ISC!, US!, NY!, UC!

= *O. borealis* de Candolle var. *sulphurea* (Porsild) Welsh

***Oxytropis sordida* (Willdenow) Persoon,** Syn. Pl. 2: 332. 1807.

Basionym: *Astragalus sordidus* Willdenow

ssp. *barnebyana* (Welsh) Jurtsev, Arctic Fl. U.S.S.R. 9(2): 109. 1986.

Basionym: *O. arctica* R. Brown var. *barnebyana* Welsh

= *O. arctica* R. Brown var. *barnebyana* Welsh

ssp. *murrayi* Jurtsev, Arctic Fl. U.S.S.R. 9(2): 179. 1986.

Type: Yukon, St. Elias Mts., Observation Mt. and vicinity, at terminus of Kaskawulsh Glacier, D. F. & B. M. Murray 522, 1966; holotype LE; isotype ALA, BRY!

= *O. arctica* R. Brown var. *murrayi* (Jurtsev) Welsh

***Oxytropis spicata* (Hooker) Standley,** Contr. U. S. Nat. Herb. 22: 373. 1921.

Basionym: *O. campestris* δ *spicata* Hooker

= *O. sericea* Nuttall var. *spicata* (Hooker) Barneby

***Oxytropis splendens* Douglas ex Hooker,** Fl. Bor.-Amer. 1: 147. 1834.

Type: Canada, on limestone rocks of the Red River, and south toward Pembina [S Manitoba], D. Douglas s.n; holotype ?; isotype OXF!, photo BRY!

Distribution: E Alaska, Yukon, N.W.T., Ontario, Manitoba, Saskatchewan, Alberta, British Columbia, Montana, North Dakota, Minnesota, Wyoming, Colorado, and New Mexico.

This species is, for the most part, readily identifiable by its copious vesture, fasciculate leaflets, and short corollas relative to calyx length. In the Alberta Rockies there occur apparent intermediates with portions of *O. campestris* var. *gracilis*. Inconclusive specimens are known between *O. splendens* and both *O. campestris* var. *johannensis* near James Bay and var. *davisii* in British Columbia and Alberta. The intermediate specimens have less copious pubescence, a tendency to fasciculate leaflets, and petal to calyx proportions intermediate from those typical of *splendens* to those typical of the *campestris* taxa.

f. *nelsonii* Gandoger, Bull. Soc. Bot. France 48: xvii. 1901.

Type: ?

= *O. splendens* Douglas

β *richardsonii* Hooker, Fl. Bor.-Amer. 1: 148. 1834.

Type: Richardson. "Franklin's Journey, Dr. Hooker"; isotype NY!, *O. oxyphylla* of Richardson, isotype GH!

= *O. splendens* Douglas

f. *strigosa* Gandoger, Bull. Soc. Bot. France 48: xvii. 1901.

Type: ?

= *O. splendens* Douglas

α *vestita* Hooker, Fl. Bor.-Amer. 1: 148. 1834

Type: Red River, D. Douglas; holotype ?

= *O. splendens* Douglas

***Oxytropis terrae-novae* Fernald,** Rhodora 30: 147, pl. 174. 1928.

Type: Newfoundland, St. John Island, peat on dry gravelly limestone barrens, M. L. Fernald et al. 28615, 31 July 1925; holotype GH!

= *O. campestris* (L.) de Candolle var. *terrae-novae* (Fernald) Barneby

***Oxytropis tschuktschorum* Jurtsev,** Bot. Journ. 53: 11, 1538. 1968.

= *O. nigrescens* (Pallas) Fischer var. *nigrescens*

***Oxytropis uralensis* δ *arctica* (R. Brown) Ledebour,** Fl. Ross. 1: 594. 1842.

Basionym: *Oxytropis arctica* R. Brown

= *O. arctica* R. Brown var. *arctica*

γ ***minor*** **Hooker**, Fl. Bor.-Amer. 1: 146. 1834.
Note: Barneby cites this name as problematical, to be excluded because of inadequate typification. The Labrador specimens cited with the original description are likely what now passes under *O. campestris* var. *terrae-novae*; the remainder is cited from dry hills and prairies in the Rock Mountains, and remains obscure.

β ***subsucculenta*** **Hooker**, Fl. Bor.-Amer. 1: 146. 1831.
Type: "Arctic seashore, to the east of the Mackenzie River," Dr. Richardson s.n.; holotype K.
= *O. borealis* de Candolle var. *borealis*

Oxytropis varians **(Rydberg) K. Schumann**, Just's Bot. Jahresb. 29: 543. 1903.
Basionym: *Aragallus varians* Rydberg
= *O. campestris* (L.) de Candolle var. *varians* (Rydberg) Barneby

Oxytropis vegana **(Cockerell) Wooton & Standley**, Contr. U. S. Nat. Herb. 16: 136. 1913.
Basionym: *Aragallus pinetorum veganus* Cockerell
= *O. sericea* Nuttall var. *sericea*

Oxytropis verruculosa **Porsild**, Bull. Nat. Mus. Canad. 121: 246. 1951.
Type: Yukon: Canol Rd.: Rose-Lapie Pass, southwest of granite mountain west of mile 116, alpine slopes from road to below summit. Elev. 5000 ft. rocky ledges, A. E. Porsild & A. J. Breitung 10072, 1 July 1944; holotype CAN!; isotype GH!, S!, US!
= *O. borealis* de Candolle var. *sulphurea* (Porsild) Welsh

Oxytropis villosa **(Rydberg) K. Schumann**, Just's Bot. Jahresb. 29: 543. 1903.
Basionym: *Aragallus villosus* Rydberg
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

Oxytropis viscida **Nuttall ex Torrey & Gray**, Flora N. Amer. 1: 341. 1838.
Type: Rocky Mountains, near the sources of the Oregon [SW Wyoming], T. Nuttall s.n., 1834; syntypes NY!, PH; and "R. Mts. Oxytropis mollis," GH!
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

var. ***hudsonica*** **(Greene) Barneby**, Proc. Calif. Acad. IV, 27: 245. 1952.
Basionym: *Aragallus hudsonicus* Greene

ssp. ***hudsonica*** **(Greene) Love & Love**, Taxon 31: 347. 1982.
Basionym: *Aragallus hudsonicus* Greene

var. ***subsucculenta*** **(Hooker) Barneby**, Proc. Calif. Acad. IV, 27: 246. 1952.
Basionym: *Oxytropis uralensis* β *subsucculenta* Hooker

var. ***viscida***

Oxytropis viscidula **(Rydberg) Tidestrom**, Contr. U.S. Nat. Herb. 25: 332. 1925.
Basionym: *Aragallus viscidulus* Rydberg
= *O. borealis* de Candolle var. *viscida* (Nuttall) Welsh

ssp. ***sulphurea*** **Porsild**, Bull. Nat. Mus. Canad. 121: 247. 1951.
Type: Yukon, Canol Rd.: Rose-Lapie R. Pass, mile 105; schist mountain east of lake. Elev. 4000, shaly cliffs by waterfall, A. E. Porsild & A. J. Breitung 10918, July 19, 1944; holotype CAN; isotype ISC!, GH!, S!, US!, NY!
= *O. borealis* de Candolle var. *sulphurea* (Porsild) Welsh

Physocalyx multiceps **Nuttall ex Gray**, Proc. Amer. Acad. 6: 234. 1864.
Type: Rocky Mountains, T. Nuttall s.n., 1834; holotype PH!; isotype NY!
= *Oxytropis multiceps* Torrey & Gray

Spiesia arctica **(R. Brown) Kuntze**, Rev. Gen. 205. 1891.
Basionym: *Oxytropis arctica* R. Brown var. *arctica*
= *Oxytropis arctica* R. Brown var. *arctica*

Spiesia arctobia **(Bunge) Kuntze**, Rev. Gen. 205. 1891.
Basionym: *Oxytropis arctobia* Bunge
= *O. nigrescens* (Pallas) Fischer var. *uniflora* (Hooker) Barneby

Spiesia bellii **Britton ex Macoun**, Can. Rec. Sc. 6: 148. 1894.
Type: Canada, Digges Island, R. Bell s.n., 15 Sept. 1884; holotype CAN!; isotype NY!; US!
= *Oxytropis arctica* R. Brown var. *bellii* (Britton) Boivin

Spiesia inflata **(Hooker) Britton**, Mem. Torrey Bot. Club 5: 201. 1894.
Basionym: *Oxytropis arctica* δ *inflata* Hooker
= *O. podocarpa* A. Gray

Spiesia lagopus **(Nuttall) Kuntze**, Rev. Gen., 206. 1891.
Basionym: *Oxytropis lagopus* Nuttall
= *Oxytropis lagopus* Nuttall

Spiesia lambertii **(Pursh) Kuntze**, Rev. Gen., 206. 1891.
Basionym: *Oxytropis lambertii* Pursh
= *Oxytropis lambertii* Pursh var. *lambertii*

var. ***sericea*** **(Nuttall) Rydberg**, Fl. Neb. 21: 43, pl. XI, figs. 107–109. 1895.
Basionym: *Oxytropis sericea* Nuttall
= *Oxytropis sericea* Nuttall

Spiesia mertensiana **(Turczaninow) Kuntze**, Rev. Gen., 206. 1891.
Basionym: *Oxytropis mertensiana* Turczaninow
= *Oxytropis mertensiana* Turczaninow

Spiesia monticola **(A. Gray) Kuntze**, Rev. Gen., 206. 1891.
Basionym: *Oxytropis monticola* A. Gray
= *Oxytropis campestris* (L.) de Candolle var. *gracilis* (A. Nelson) Barneby

Spiesia multiceps **(Torrey & Gray) Kuntze**, Rev. Gen., 206. 1891.
Basionym: *Oxytropis multiceps* Torrey & Gray
= *Oxytropis multiceps* Torrey & Gray

Spiesia nana **(Nuttall) Kuntze**, Rev. Gen., 206. 1891.
Basionym: *Oxytropis nana* Nuttall
= *Oxytropis nana* Nuttall

Spiesia nigrescens **(Pallas) Kuntze**, Rev. Gen., 206. 1891.
Basionym: *Astragalus nigrescens* Pallas
= *Oxytropis nigrescens* (Pallas) Fischer var. *nigrescens*

Spiesia oreophila **(A. Gray) Kuntze,** Rev. Gen., 206. 1891.
Basionym: *Oxytropis oreophila* A. Gray
= *Oxytropis oreophila* A. Gray

Spiesia parryi **(A. Gray) Kuntze,** Rev. Gen., 206. 1891.
Basionym: *Oxytropis parryi* A. Gray
= *Oxytropis parryi* A. Gray

Spiesia podocarpa **(A. Gray) Kuntze,** Rev. Gen., 206. 1891.
Basionym: *Oxytropis podocarpa* A. Gray
= *Oxytropis podocarpa* A. Gray

Spiesia splendens **(Douglas) Kuntze,** Rev. Gen., 207. 1891.
Basionym: *Oxytropis splendens* Douglas
= *Oxytropis splendens* Douglas

Spiesia viscida **(Nuttall) Kuntze,** Rev. Gen., 206. 1891.
Basionym: *Oxytropis viscida* Nuttall
= *Oxytropis borealis* de Candolle var. *viscida* (Nuttall) Welsh

LITERATURE CITED

BARNEBY, R. C. 1952. A revision of the North American species of *Oxytropis* DC. Proceedings of the California Academy of Science IV, 27: 177–312.

BOIVIN, B. 1962. Etudes sur les *Oxytropis* DC. I. *Oxytropis deflexa* (Pallas) DC. Svensk Botaniska Tidskrift 56: 496–500.

_____. 1967. Etudes sur les *Oxytropis* DC. II. Naturaliste Canadiene 94: 73–78.

BUNGE, A. 1874. Species Generis *Oxytropis*, DC. Memoires l'Academie Imperiale des Sciences de St. Petersbourg VII, 22(1): 1–166.

ELISENS, W. J., AND J. G. PACKER. 1980. A contribution to the taxonomy of the *Oxytropis campestris* complex in northwestern North America. Canadian Journal of Botany 58: 1820–1831.

_____. 1982. Typification of *Oxytropis monticola*. Canadian Journal of Botany 60: 1580–1582.

GRAY, A. 1884. A revision of the North American species of *Oxytropis* DC. Proceedings of the American Academy 20: 1–7.

JURTSEV, B. A. 1986. *Oxytropis* DC. Pages 61–146 *in* A. A. Korobkov, M. V. Sokolova, N. N. Taraskina, and B. A. Jurtsev, Arctic flora U.S.S.R 9(2). 187 pp.

PORSILD, A. E., AND W. J. CODY. 1980. *Oxytropis* DC. Pages 438–442 *in* Vascular plants of the continental Northwest Territories, Canada. National Museum of Natural Sciences, National Museums of Canada. 667 pp.

VASIL'CHENKO, I. T., B. A. FEDCHENKO, AND B. K. SHISHKIN. 1948. *Oxytropis* DC. *in* Flora U.S.S.R 13: 1–229.

WELSH, S. L. 1967. Legumes of Alaska II: *Oxytropis* DC. Iowa State Journal of Science 41: 277–303.

_____. 1974. *Oxytropis* DC. Pages 275–282 *in* Anderson's flora of Alaska and adjacent parts of Canada. Brigham Young Press, Provo, Utah. 724 pp.

_____. 1977. On the typification of *Oxytropis leucantha* (Pallas) Pers. Taxon 21: 155–157.

_____. 1987. *Oxytropis* DC. Pages 396–398 *in* S. L. Welsh, N. D. Atwood, S. Goodrich, and L. C. Higgins, A Utah flora. Great Basin Naturalist Memoirs 9. 984 pp.

Received 19 August 1991
Accepted 15 October 1991

Great Basin Naturalist 51(4), 1991, pp. 397–403

ALKALOIDAL RELATIONSHIPS IN THE GENUS *ARCTOMECON* (PAPAVERACEAE) AND HERBIVORY IN *A. HUMILIS*

Douglas E. Raynie[1], Deanna R. Nelson[2], and Kimball T. Harper[2]

Abstract.—The previously reported alkaloids (including protopines, benzophenanthridines, tetrahydrobenzylisoquinolines, and protoberberines) of the genus *Arctomecon* (Papaveraceae) are discussed in relation to their distribution in the plant kingdom, in the Papaveraceae, and among the three species of *Arctomecon*. The biological activity of these alkaloids is discussed, and possible implications for herbivore and plant-insect interactions in *A. humilis* are presented.

Key words: Arctomecon, *Papaveraceae, alkaloids, herbivory.*

The Papaveraceae genus *Arctomecon* contains only three species, all rare endemics in the western United States. The geographic distribution of the bear or desert poppies, *Arctomecon* spp., is shown in Figure 1. The great bear poppy (*A. merriamii* Coville) is the most common of these species, extending from the Las Vegas area of southern Nevada to the Death Valley region of southeastern California. *A. californica* Torr. & Fremont, the yellow bear poppy, was once common in the vicinity of Las Vegas and the Lake Mead region of southern Nevada and northwestern Arizona, but numbers have rapidly declined due to habitat loss. The dwarf bearclaw poppy (*A. humilis* Coville) is disjunct from the other species, growing exclusively in Washington County, Utah. *A. humilis* has been declared an endangered species by the U.S. Fish and Wildlife Service under the Endangered Species Act of 1973 as amended, while both *A. merriamii* and *A. californica* are presently under consideration for such protection. Habitat requirements and ecological relations of *A. humilis* and *A. californica* have been studied by Meyer (1986, 1989) and Nelson (1989). Both are obligate gypsophiles. Unlike the other two species, *A. merriamii* is not restricted to gypsum-rich soils but often occurs on shallow soils derived from limestone.

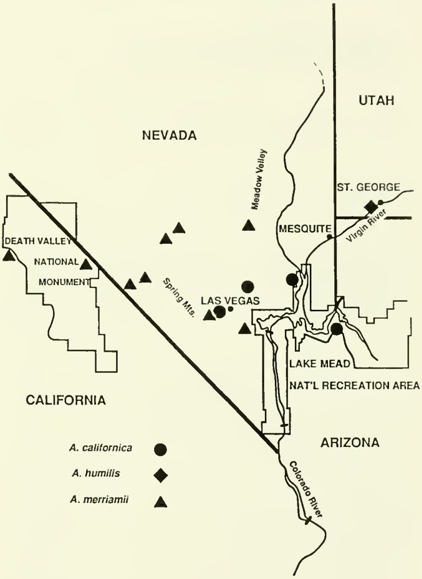


Fig. 1. Distribution of *Arctomecon* (Papaveraceae).

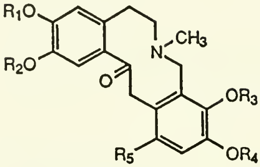
We have reported elsewhere (Raynie et al. 1990) the alkaloid chemicals found in this genus. Sixteen different isoquinoline alkaloids from four classes were found, and the structural details (for 14 of those alkaloids) were determined. The structures of the alkaloids known for these species are shown in Figure 2. The alkaloids identified include the protopines allocryptopine, protopine, cryptopine, and 12-methoxyallocryptopine; the benzophenanthridines chelerythrine,

---

[1] Department of Chemistry, Brigham Young University, Provo, Utah 84602. Present address: Procter & Gamble Company, Corporate Research Division, Miami Valley Laboratories, Box 398707, Cincinnati, Ohio 45239-8707.

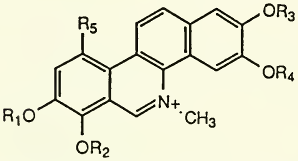
[2] Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602.

PROTOPINES

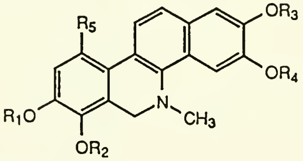


Allocryptopine: R_1-R_2 = CH_2 R_3 = R_4 = CH_3 R_5 = H
Protopine: R_1-R_2 and R_3-R_4 = CH_2 R_5 = H
Cryptopine: R_1 = R_2 = CH_3 R_3-R_4 = CH_2 R_5 = H
12-Methoxyallocryptopine: R_1-R_2 = CH_2 R_3 = R_4 = CH_3 R_5 = OCH_3

BENZOPHENANTHRIDINES



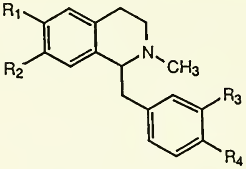
Chelerythrine: R_1 = R_2 = CH_3 R_3-R_4 = CH_2 R_5 = H
Sanguinarine: R_1-R_2 and R_3-R_4 = CH_2 R_5 = H
Sanguirubine: R_1-R_2 = CH_2 R_3 = R_4 = CH_3 R_5 = OCH_3



Dihydrochelerythrine
Dihydrosanguinarine

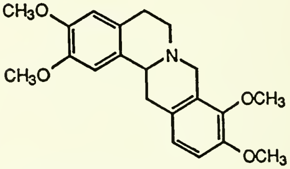
Fig. 2. Structures of alkaloids found in *Arctomecon* (Papaveraceae).

TETRAHYDROBENZYLISOQUINOLINES



Reticuline: R_1 = R_4 = OCH_3 R_2 = R_3 = OH
Pseudolaudanine: R_1 = OH R_2 = R_3 = R_4 = OCH_3
Armepavine: R_1 = R_2 = OCH_3 R_3 = H R_4 = OH

PROTOBERBERINES



Tetrahydropalmatine
N-Methyltetrahydropalmatine

Fig. 2 continued.

sanguinarine, sanguirubine, dihydrochelerythrine, and dihydrosanguinarine; the tetrahydrobenzylisoquinolines armepavine, pseudolaudanine, and reticuline; and the protoberberines tetrahydropalmatine and N-methyltetrahydropalmatine. One of these, 12-methoxyallocryptopine, was reported for the first time in our earlier study (Raynie et al. 1990). In this contribution, the alkaloids of *Arctomecon* are compared with the alkaloids of other genera of Papaveraceae. The possible values of these alkaloids to the species that produce them are also discussed.

DISTRIBUTION AND PHYSIOLOGICAL ACTIVITY OF *ARCTOMECON* ALKALOIDS

The presence of alkaloids (i.e., the ability to synthesize or accumulate alkaloids) occurs in many lineages within the plant kingdom, especially among the dicotyledons. A brief summary of the distribution in the plant kingdom of the alkaloid types reported in *Arctomecon* and their known physiological activity follows.

Cordell (1981) reviewed the phylogenetic distribution and pharmacological activity of alkaloids. In addition to the Papaveraceae, the protopines are found in four plant families (Berberidaceae, Fumariaceae, Ranunculaceae, and Rutaceae) and are represented by about 20 compounds. The physiological effects of the protopines on mammals include active dilation of coronary vessels and local anesthetic effects (Preininger 1975). The benzophenanthridines are limited to the

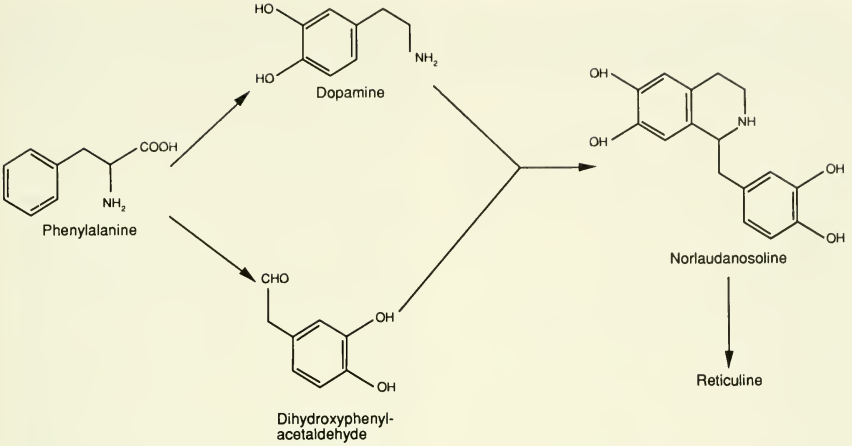


Fig. 3. Initial steps in biosynthetic scheme of Papaveraceae alkaloids from phenylalanine (after Preininger 1986).

Papaveraceae, Fumariaceae, and Rutaceae. Chelerythrine and sanguinarine, representative benzophenanthridines found in *Arctomecon*, are reported to have cytotoxic, antifungal, antiprotozoal, antibacterial, and potential anticancer activity (Cordell 1981). The tetrahydrobenzylisoquinolines, especially reticuline, are best known as biosynthetic intermediates for many other alkaloids. The protoberberines are among the most widely distributed of the isoquinoline alkaloids, occurring in nine plant families, including Annonaceae, Berberidaceae, Fumariaceae, Lauraceae, Menispermaceae, Papaveraceae, and Rutaceae. Over 40 protoberberines are known. They display at least three types of biological activity; antimicrobial, stimulation of uterine contractions, and antileukemic and antineoplastic.

RELATIONSHIP OF *ARCTOMECON* ALKALOIDS IN THE PAPAVERACEAE

The Fumariaceae and Papaveraceae are closely related families in the order Papaverales. According to Cronquist (1981), the poppy family, Papaveraceae, contains 25 genera and about 200 species. This family is unusual in that all of its species are reported to contain alkaloids (Pelletier 1970). A major feature of both the Fumariaceae and the Papaveraceae is the presence of alkaloids derived from tetrahydroisoquinolines (Preininger 1986). Preininger (1986) has reviewed, by genus, the alkaloids of the Papaveraceae and demonstrated how the biodiversity of the poppy family is reflected in its chemical diversity. The isoquinoline alkaloids can be biosynthesized from the amino acid phenylalanine by the condensation of dopamine with 3,4-dihydroxyphenylacetaldehyde followed by the Mannich condensation, yielding norlaudanosoline. From norlaudanosoline, intermediates such as reticuline and orientaline are formed in the biosynthesis of a variety of isoquinoline types (Preininger 1986). This biosynthetic scheme is shown in Figure 3.

According to Preininger's review (1986), protoberberines, benzophenanthridines, and protopines are the most widespread alkaloids in the Papaveraceae, present in almost all genera. Quaternary tetrahydroprotoberberines serve as intermediates in the biosynthetic processes that produce the foregoing alkaloids. Consequently these alkaloids were considered as a chemotaxonomically significant characteristic of the Papaveraceae. As discussed earlier, alkaloids from each of these classes, as well as tetrahydrobenzylisoquinoline alkaloids, occur in *Arctomecon*. Table 1 shows the distribution of the alkaloids found in *Arctomecon* among other Papaveraceae

TABLE 1. Distribution of alkaloids known to occur in *Arctomecon* among other genera of the Papaveraceae. The numbers at the head of each column represent *Arctomecon* alkaloids, each of which is identified in the footnote.

	Alkaloid												
	A[a]			B					C			D	
Genus	1	2	3	4	5	6	7	8	9	10	11	12	13
Argemone	x	x	x	x	x	x	x		x			x	
Bocconia	x	x		x	x	x	x						
Chelidonium	x	x		x	x	x	x						
Dendromecon	x	x				x	x						
Dicranostigma	x	x		x		x							
Eschscholtzia	x	x	x	x	x	x							
Glaucium	x	x	x	x	x	x	x			x		x	
Hunnemannia	x	x		x		x							
Hylomecon	x	x		x		x							
Macleaya	x	x		x		x							
Meconella		x											
Meconopsis	x	x	x			x							
Papaver	x	x	x	x		x	x		x	x			
Platystemon		x		x		x							
Roemeria		x											
Romneya		x		x		x	x			x			
Sanguinaria	x	x		x		x		x					
Stylomecon	x	x	x	x		x							
Stylophorum	x	x	x	x		x							

[a] Key: A = protopines, B = benzophenanthridines, C = tetrahydrobenzylisoquinolines, D = protoberberines, 1 = allocryptopine, 2 = protopine, 3 = cryptopine, 4 = chelerythrine, 5 = dihydrochelerythrine, 6 = sanguinarine, 7 = dihydrosanguinarine, 8 = sanguirubine, 9 = armepavine, 10 = reticuline, 11 = pseudolaudanine, 12 = tetrahydropalmatine, 13 = N-methyltetrahydropalmatine. Compiled from Preininger (1986), Raffauf (1970), Stermitz (1989), Willaman and Li (1970), and Willaman and Schubert (1961).

genera. The alkaloids of the Papaveraceae genera *Canbya* and *Eomecon* have yet to be studied; thus those genera are not included in Table 1. The alkaloids 12-methoxyallocryptopine, pseudolaudanine, and N-methyltetrahydropalmatine are found in the Papaveraceae only in *Arctomecon* at this time. The tetrahydrobenzylisoquinolines and the protoberberines of *Arctomecon* are shared only with *Argemone* and *Romneya* (tetrahydrobenzylisoquinolines only) among the genera endemic to western North America (*Argemone, Dendromecon, Eschscholtzia, Platystemon*, and *Romneya*). The tetrahydrobenzylisoquinolines and the protoberberines are also shared with the genera *Glaucium* (European) and *Papaver* (tetrahydrobenzylisoquinolines only), a genus widespread in the Northern Hemisphere. It is interesting to note that protopine is found in all and allocryptopine, chelerythrine, and sanguinarine in nearly all genera of Papaveraceae. According to Santavy (1970), sanguinarine-type benzophenanthridines are the most widely distributed alkaloids in the Papaveraceae. As indicated in Table 1, *Meconella* and *Roemeria* are the only genera that do not contain at least one of the five benzophenanthridines reported in *Arctomecon*. *Dendromecon* and *Meconopsis* are the only genera in which sanguinarine is reported in the absence of chelerythrine; however, the results for *Dendromecon* are preliminary, and benzophenanthridines other than those reported in Table 1 (i.e., sanguinarine and dihydrosanguinarine) may be present in trace amounts (F. R. Stermitz, unpublished data, 1989). It is not surprising that the dihydro- analogues of benzophenanthridines (i.e., dihydrochelerythrine and dihydrosanguinarine) are reported only in the presence of the parent compounds. Among the *Arctomecon* alkaloids, 12-methoxyallocryptopine, pseudolaudanine, and N-methyltetrahydropalmatine have not been reported elsewhere in the Papaveraceae. As stated earlier, 12-methoxyallocryptopine is a new alkaloid reported only in *Arctomecon*. It is interesting that 12-methoxyallocryptopine occurs in significant quantities in all species of *Arctomecon* but is absent in all other Papaveraceae genera. Other protopines are widespread in the Papaveraceae. We previously speculated (Raynie et al. 1990) that a new biosynthetic pathway for 12-methoxyallocryptopine may be present in *Arctomecon*, evidenced by an accumulation of protopine-type alkaloids and a relatively low content of benzophenanthridines in *Arctomecon* relative to related genera. The absence of pseudolaudanine and N-methyltetrahydropalmatine in other Papaveraceae is not too surprising, since they are present in *Arctomecon* in minor amounts and in only one or two species. Due to the role of tetrahydrobenzylisoquinolines and tetrahydroprotoberberines as biosynthetic intermediates, it would not be unreasonable to expect the presence of pseudolaudanine and n-methyltetrahydropalmatine in other Papaveraceae genera in amounts too small to be detected.

ALKALOID DISTRIBUTION IN *ARCTOMECON* AND POSSIBLE IMPLICATIONS

Absolute quantities of endogenous alkaloids are expected to vary with such factors as stage of plant development, tissue considered, and environmental factors, as well as

TABLE 2. Tissue distribution of alkaloids found in *Arctomecon*.

Alkaloid	*A. humilis*				*A. californica*				*A. merriamii*			
PROTOPINES												
Protopine	C[a]	R	L	O	C	R	L	O	C	R	L	O
Allocryptopine	C	R	L	O	C	R	L	O	—	R	L	—
12-Methoxyallocryptopine	C	—	—	—	—	R	—	—	C	R	—	—
Cryptopine	—	R	—	—	—	—	—	—	—	—	—	—
BENZOPHENANTHRIDINES												
Unknown	—	R	—	—	—	R	—	—	—	R	—	—
Sanguinarine	—	R	—	—	—	R	—	—	—	R	—	—
Dihydrosanguinarine	—	R	—	—	—	R	—	—	—	R	—	—
Chelerythrine	—	R	—	—	—	—	—	—	—	—	—	—
Dihydrochelerythrine	—	R	—	—	—	—	—	—	—	—	—	—
Sanguirubine	—	R	—	—	—	—	—	—	—	—	—	—
Unknown	—	—	—	—	—	R	—	—	—	—	—	—
TETRAHYDROBENZYLISOQUINOLINES												
Armepavine	C	—	—	O	—	—	—	—	—	—	—	O
Reticuline	C	—	—	O	—	—	—	—	—	—	—	—
Pseudolaudanine	—	—	—	—	—	—	—	—	—	—	—	O
PROTOBERBERINES												
N-methyltetrahydropalmatine	—	—	L	—	—	—	L	—	—	—	—	—
Tetrahydropalmatine	—	—	L	O	—	—	—	—	—	—	—	—

[a] Key: C capsule, R root, L leaf, O other (primarily stalk, also flowers and buds). Compiled from Raynie et al. (1990)

genetic differences. For this reason, absolute statements concerning the alkaloid content of *Arctomecon* must be made with the warning that these statements may be only partially correct, since our determination of the alkaloid content of *Arctomecon* is best construed as a "snapshot in time" rather than a truly definitive study. This warning was articulated by Robinson (1979):

> This ontogenic variation should be a warning to anyone who searches for a role of alkaloids in ecological interactions, for it is the alkaloid content at the exact time and place of any presumed interaction that must be determined. . . . For the field ecologist it is important to recognize that one population of a species may have a different alkaloid content than another population growing at a different location.

In an early study on the alkaloids of *A. californica*, Stermitz and Muralidharan (1967) reported that protopine and allocryptopine were present in approximately equal amounts, accounting for around 95% of the total alkaloid content. Muralidharan (1969) also reported that the total alkaloid content in *A. californica* was 0.4% and that, in addition to protopine and allocryptopine, at least three additional basic alkaloids and one quaternary alkaloid were present. However, these alkaloids were not identified. These results are similar to those we have reported (Raynie et al. 1990). In all species of *Arctomecon*, divided by tissue type, allocryptopine and protopine combined to account for 60–100% of the total alkaloid content. With the exception of *A. californica* capsule and root tissues, allocryptopine is present at much higher levels than protopine, and, in *A. merriamii*, root tissue is the only significant source of protopine.

A general rule of alkaloid distribution in plants is that they tend to accumulate in actively growing tissues and latex vessels and that alkaloid content increases rapidly at the time of cell enlargement and vacuolization and then declines slowly during senescence (Robinson 1979). The alkaloid distribution in *Arctomecon* is presented by tissue type in Table 2. Our results for *Arctomecon* showed that the highest concentration of alkaloids was in the capsule and the lowest was in the root, although for *A. californica* the amount of total alkaloids was more evenly distributed among tissues. Although the alkaloid content of the root material was lower than in other tissues, root tissue was found to contain the greatest variety of different alkaloids, and the benzophenanthridine alkaloids were limited exclusively to root tissue. Other generalizations from our limited sample include the facts that the allocryptopine/protopine ratio is greater in the leaf and stalk tissues than in capsule and root tissues and that *A. californica* and

A. merriamii are much simpler, in terms of alkaloid makeup, than *A. humilis*. The tetrahydrobenzylisoquinolines and tetrahydroprotoberberines, possible biosynthetic intermediates, were found scattered in trace amounts in all tissues except the root. However, conclusions cannot be drawn from this observation, since it is well known that the site of alkaloid accumulation is often not the site of synthesis.

Robinson (1979) has suggested that alkaloids in leaf and stem tissue render those tissues less palatable to herbivores. A population of over 400 individuals of *A. humilis* has been inventoried at four- to six-week intervals (and with greater frequency during the flowering season) from February 1987 to the present (Nelson 1989). Other *A. humilis* populations were observed less regularly during this same time period. At each observation period, we searched for evidences of herbivore predation in all individuals. Herbivory was found to be uncommon in *A. humilis* plants, and such herbivory as was noted was attributed to two sources: rabbits and insects. In the late summer and fall of 1987, considerable use by rabbits was observed. Rabbit herbivory has been observed in only a few isolated incidents since that time. Typically, leaves were clipped near the base, and a pile of "harvested" leaves usually occurred near the plant. In all cases clipped leaves were accompanied by rabbit feces located within 40–50 cm of the affected plant. Of the 84 plants exhibiting herbivory, 82% died. While overall mortality in the population was high (58%) during 1987, mortality among the rabbit-damaged plants was significantly greater than among ungrazed plants. Nevertheless, it is not possible to attribute a cause-and-effect relationship to such data. While it may seem apparent that herbivory was the cause of mortality, it is possible that decadence of the foliage rendered the tissue more palatable to rabbits.

Robinson (1979) also noted the role of alkaloids, especially steroidal alkaloids, in plant-insect interactions. Insect damage to *A. humilis* was minimal on the study plot throughout the three years of observation. The most commonly observed insect was a small mealybug tentatively identified as *Spilococcus atriplicis* at the California Department of Food and Agriculture (Riley Nelson, personal communication, 1990). The organism itself is very minute and rudimentary, unable to fly or walk. Its infestation is marked by a cottony mass that shelters a few of the insects at the base of individual leaves. The infection sites are buried well into the thatch of leaves. The first infestations of this type were noted in April 1989. Twenty plants, in two subpopulations, harbored the insect. In July only 14 plants displayed the cottony masses. Only 8 plants harbored the insects in October. The number of infected plants increased to 13 in December 1989. Effects of the insect on *A. humilis* plants appear to be variable, but in most cases an increase in the amount of decadent leaf tissue was observed. *Spilococcus* spp. are sucking insects known to feed on plant juices. Affected leaves gradually turn brown and abscise. Of the 20 plants infected in April 1989, 3 had died by December; each of these individuals had exhibited less than 30% decadent tissue at the first sign of infestation. Only 4 of the 20 infected plants exhibited greater than 50% decadent tissue in April, but 12 had greater than 50% dead tissue by December. The condition of three plants seemed to improve after infestation. Infestations moved from plant to plant through time; only 7 of the 20 plants infected in April still showed signs of infestation in December.

McKenzie (1967) notes that the Southern California mealybug (*S. atriplicis*) infects *Baccharis* spp., *Eriogonum inflatum*, *Pleuchea sericea*, *Haplopappus* spp., and *Eriogonum* spp. in California and *Atriplex canescens* in New Mexico. To our knowledge, none of these hosts are reported to contain significant amounts of alkaloids. However, *Spilococcus* is morphologically similar to the mealybug genera *Phenacoccus* and *Pseudococcus*. *Phenacoccus eschscholtziae* and *Pseudococcus obscurus* are both known to infect the California poppy (*Eschscholtzia californica*).

Mealybugs are known to have a host of symbiotic relationships with various ants (McKenzie 1967). Seed-offering experiments (D. R. Nelson and K. T. Harper, unpublished data, 1989) have shown that ants appear to be the principal biological dispersal agent of *A. humilis* seeds. Thus ants are regularly associated with *A. humilis* plants, and ants have been reported to sometimes move mealybugs from one host plant to another (McKenzie 1967). It is thus possible that ants spread the infestation from plant to plant across the barren gypsum soil.

CONCLUSIONS

Arctomecon species are similar to most other Papaveraceae genera in respect to protopine and benzophenanthidine alkaloids, but they also contain tetrahydrobenzylisoquinoline and protoberberine alkaloids that have not been reported for most other poppy genera. The tetrahydrobenzylisoquinoline-type alkaloids are also known from the genera *Argemone* (primarily western North American), *Glaucium* (European), *Papaver* (circumboreal), and *Romneya* (southern California and adjacent Mexico). The protoberberine alkaloids are known only for the genera *Argemone* and *Glaucium* in the Papaveraceae. The diverse alkaloid content of the *Arctomecon* species may be related to the light herbivory observed on these evergreen species in the desert environment.

ACKNOWLEDGMENTS

This work was supported by a Utah Native Plant Society grant and a U.S. Bureau of Land Management contract. The authors are indebted to Dr. Riley Nelson, University of Texas at Austin, for assistance in finding an entomologist to provide identification of the mealybug that attacks *A. humilis* and for discussions concerning *Spilococcus atriplicis*. The mealybug was identified by Dr. Ray J. Gill of the California Department of Food and Agriculture, Sacramento. Dr. Frank R. Stermitz, Colorado State University, generously shared his knowledge concerning alkaloid relationships in the Papaveraceae.

LITERATURE CITED

CORDELL, G. A. 1981. Introduction to the alkaloids: a biogenic approach. John Wiley and Sons, New York.

CRONQUIST, A. 1981. An integrated system of classification of flowering plants. Columbia University Press, New York.

MCKENZIE, H. L. 1967. Mealybugs of California. University of California Press, Berkeley.

MEYER, S. E. 1986. The ecology of gypsophile endemism in the eastern Mojave Desert. Ecology 67: 1303–1313.

______. 1989. Life history of *Arctomecon californica* (Papaveraceae), a Mojave Desert endemic perennial herb. In manuscript.

MURALIDHARAN, V. P. 1969. I. Alkaloids of *Arctomecon californica*. II. Investigation of the photochemical behavior of some ketones. Unpublished dissertation, Utah State University, Logan.

NELSON, D. R. 1989. Site characteristics and habitat requirements of the endangered dwarf bear-claw poppy (*Arctomecon humilis* Coville, Papaveraceae) and demographic and seed bank biology of *Arctomecon humilis* (Papaveraceae), a short-lived perennial. Unpublished master's thesis, Brigham Young University, Provo, Utah.

PELLETIER, S. 1970. Chemistry of the alkaloids. Van Nostrand Reinhold, New York.

PREININGER, V. 1975. The pharmacology and toxicology of the Papaveraceae alkaloids. Pages 207–261 *in* R. H. F. Manske, ed., The alkaloids. Vol. 15. Academic Press, New York.

______. 1986. Chemotaxonomy of Papaveraceae and Fumariaceae. Pages 1–98 *in* A. Brossi, ed., The alkaloids. Vol. 29. Academic Press, New York.

RAFFAUF, R. F. 1970. Handbook of alkaloids and alkaloid-containing plants. Wiley-Interscience, New York.

RAYNIE, D. E., M. L. LEE, D. R. NELSON, K. T. HARPER, E. W. MEAD, AND F. R. STERMITZ. 1990. Alkaloids of *Arctomecon* species (Papaveraceae). 12-methoxyallocryptopine, a new protopine-type alkaloid. Biochemical Systematics and Ecology 18: 45–48.

ROBINSON, T. 1979. The evolutionary ecology of alkaloids. Pages 413–448 *in* G. A. Rosenthal and D. A. Janzen, eds., Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.

SANTAVY, F. 1970. Papaveraceae alkaloids. Pages 333–454 *in* R. H. F. Manske, ed., The alkaloids. Vol. 12. Academic Press, New York.

STERMITZ, F. R., AND V. P. MURALIDHARAN. 1967. Alkaloids of the Papaveraceae VI. Protopine and allocryptopine from *Arctomecon californica*. Journal of Pharmaceutical Science 56: 762.

WILLAMAN, J. J., AND H.-L. LI. 1970. Alkaloid-bearing plants and their contained alkaloids, Part II. Lloydia 33(3A).

WILLAMAN, J. J., AND B. G. SCHUBERT. 1961. Alkaloid-bearing plants and their contained alkaloids. U.S. Department of Agriculture, Technical Bulletin 1234. Washington, D.C.

Received 20 March 1991
Accepted 19 August 1991

Great Basin Naturalist 51(4), 1991, pp. 404–410

SCANNING ELECTRON MICROSCOPIC STUDY OF THE MALE GENITALIA OF THE NORTH AMERICAN ALDERFLY GENUS *SIALIS* (MEGALOPTERA: SIALIDAE)

Michael F. Whiting[1]

ABSTRACT.—Scanning electron micrographs are presented for 14 species of the North American alderfly *Sialis: americana, arvalis, californica, contigua, cornuta, hamata, iola, joppa, mohri, nevadensis, occidens, rotunda, vagans,* and *velata.* Male genitalic characters are described for use in species identification.

Key words: Sialis, *Sialidae, Megaloptera, Neuroptera, SEM, alderflies.*

There are currently 24 biological species of *Sialis* recognized from North America (Ross 1937, Townsend 1939, Flint 1964, Whiting 1991). Ross (1937) was the first to illustrate and compare the genitalic characters among many species of alderflies. While both Canterbury (1978) and Evans (1971) have concentrated studies on the larvae of North American *Sialis*, since the work of Ross (1937) no serious study has compared the male genitalia among all the North American species. A clear understanding of genitalic characters is essential for proper species identification; consequently, there is a critical need to reexamine male genitalia within the genus *Sialis*.

During a study of the phylogenetic relationships among the North American species of *Sialis*, I used electron microscopy to evaluate minute genitalic characters with greater clarity. The purpose of this paper is to present the electron micrographs and brief descriptions of the species groups and the diagnostic genitalic characters for 14 species of *Sialis*. Because the micrographs better illustrate many of the structures used by Ross (1937) in his key to the North American species of *Sialis* and also show many new and important characters, this paper should be useful for species identification.

METHODS AND MATERIALS

Over 4000 specimens of North American adult *Sialis* were dissected and examined with a light microscope to evaluate genitalic characters among many individuals from the 14 different species. From each species a male specimen was specially dissected for SEM study. Collection data for the specimens used in this study are as follows: *americana* (Rambur): WISCONSIN, Grant Co., Wyalusing State Park, 26 June 1957, A. L. Thorne; *arvalis* Ross: CALIFORNIA, Santa Clara Co., San Jose, Alum Rock Park, 19 April 1987, N. D. Penny; *californica* Banks: CALIFORNIA, Napa Co., Napa, 2 May 1948, H. P. Chandler; *contigua* Flint: VIRGINIA, Smyth Co., North Fork of Holston River, Route 42, near junction Route 633, 5 May 1981, B. C. Kondratieff; *cornuta* Ross: CANADA, Alberta, Konanaskis beaver ponds near Lusk Creek, 6 May 1969, T. G. Leischner; *hamata* Ross: UTAH, Wasatch Co., Bryants Fork Creek near Strawberry Reservoir, 6 June 1988, M. F. Whiting; *iola* Ross: VIRGINIA, Montgomery Co., Isaac Walton Park Pond, 11 May 1977, S. Mudre; *joppa* Ross: NEW HAMPSHIRE, Coos Co., Ellis River, Hwy. 16, Pinkham Notch, 7 June 1980, Baumann & Earnshaw; *mohri* Ross: MINNESOTA, St. Louis Co., Lake Jeanette, 22 June 1964, H. B. Mills; *nevadensis* Davis: CALIFORNIA, El Dorado Co., Blodgett Forest, 31 May 1969, D. Levin; *occidens* Ross: CALIFORNIA, Mariposa Co., Miami Ranger Station, 23 May 1942, S. H. Benedict; *rotunda* Banks: OREGON, Klamath Co., Wood River Spring, 12 June 1964, J. Schuh; *vagans* Ross: VIRGINIA, Brunswick Co., Greef Creek, U.S. 58 bridge,

---

[1] Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah 84602. Present address: Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999.

25 April 1982, B. C. Kondratieff; *velata* Ross: MINNESOTA, Louis Co., Eaglenest Lake, 1 June 1959, W. V. Balduff.

For specimens preserved on pins, the last four segments of the abdomen were removed and placed in a warm solution of 10% KOH (potassium hydroxide) for 20 minutes until the abdominal cuticle was softened and the genitalia became clearly visible. Specimens preserved in alcohol did not require treatment with the KOH solution. The abdomens were placed in an ultrasonic cleaning unit for 15 seconds to dislodge any foreign material from their surfaces. They were then removed from the cleaning unit and further dissected as needed to expose the genitalia. The abdomens were serially dehydrated in a series of ethanol concentrations (70%, 80%, 90%, 100% for 15 minutes each) and then placed in a solution of acetone over calcium sulfate crystals (2 hours). They were next critical-point-dried, mounted on aluminum stubs, and gold-plated in a Polaron DC sputter coater in preparation for SEM examination at 10 kv.

GENITALIC STRUCTURES

SEM analysis illustrates with greater clarity the genitalic structures useful for species identification within the *Sialis*. Ross (1937) used purely descriptive names for *Sialis* genitalia. Since a definite homology for the genitalia of alderflies with those of other insect groups has not yet been proposed, and since all other species descriptions of *Sialis* have relied upon these same names (Townsend 1939, Flint 1964, Whiting 1991), for the sake of consistency this paper will use Ross's descriptive names.

The male genitalia of *Sialis* consist of three major parts: the lateral, genital, and terminal plates. The lateral plates are a pair of ovoid plates just posterior to sternum 9 (Fig. 1c). These plates are contiguous mesally in most species and covered with dense setae. In some species these plates are modified into large arms bearing coarse setae (Fig. 9). The genital plate is a single sclerotized plate found posterior to the lateral plates and anterior to the terminal plates (Fig. 1b). In many species this plate is divided into two major arms that vary in size and length among species. Basally, the genital plate is either fused to the basal portion of the terminal plate (Infumata species group) or attached to a membranous wall. Because the shape of the genital plate is highly species specific, it is the most diagnostic character for determining species identity. However, because it is also the smallest genitalic structure and is usually concealed beneath the terminal and lateral plates, it is often the most difficult structure to observe. The terminal plate is a single plate on the caudal end of the abdomen circling the borders of the anus (Fig. 1a). The dorsal margin of this plate is reduced while the ventral margin is often cleft, bilobed, or modified into single or double arms. Every species and species group of *Sialis* has a unique combination of modifications of these genitalic structures, making species identification rather simple and straightforward.

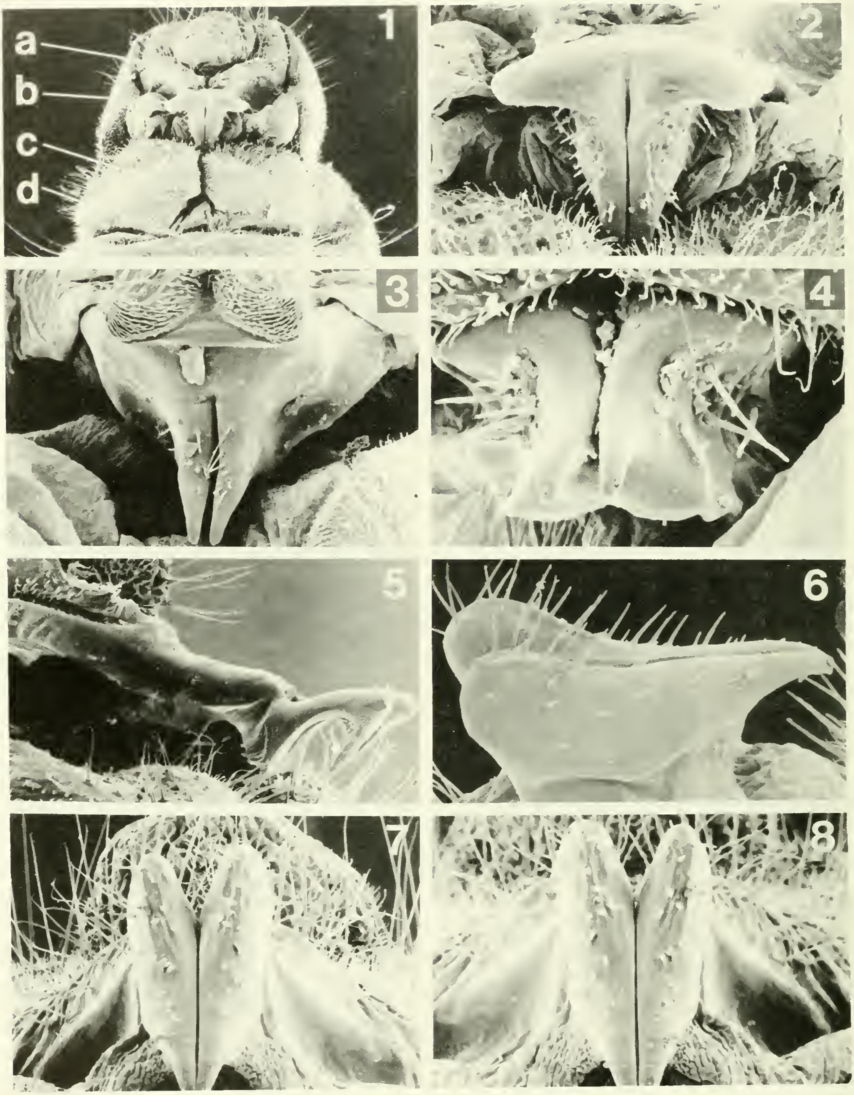
CALIFORNICA GROUP

The Californica species group consists of three eastern species (*driesbachi* Flint, *iola* Ross, and *joppa* Ross) and six western species (*arvalis* Ross, *bilobata* Whiting, *californica* Banks, *cornuta* Ross, *hamata* Ross, and *occidens* Ross). This group is characterized by a conspicuous bulbous evagination on tergum 9, reduced sternum 9, and a greatly reduced genital plate clothed sparsely with setae.

Sialis californica Banks.—From a lateral aspect (Fig. 6), the genital plate is saddle-shaped and lobed behind the point of basal attachment. The size of this lobe appears to vary in different populations, with a tendency to gradually decrease as the distributions become more northern. From the dorsal aspect, the arms of the genital plate are contiguous mesally and moderately covered with setae (Fig. 8).

Sialis occidens Ross.—The basal portion of the genital plate projects above the apex of the terminal plate (Fig. 1). The genital plates are superficially shaped like *S. californica* except that the basal portions are flanged laterad and devoid of any setae (Fig. 2) and the genital plate is not lobed behind the point of articulation with the basal membrane.

Sialis hamata Ross.—The ventral margin of the terminal plate bears a dark, elongate sclerotization that projects from the base of the terminal plate and hinges basally to the genital plate (Fig. 5). The length of this neck is reduced in northern populations. The genital



Figs. 1–8. Male genitalia of *Sialis* spp.: 1, *occidens* Ross, a. terminal plate, b. genital plate, c. lateral plate, d. sternum 9 (ventral); 2, *occidens* Ross, genital plate (ventral); 3, *cornuta* Ross, genital plate (ventral); 4, *arvalis* Ross, genital plate (ventral); 5 and 7, *hamata* Ross, genital plate (anterolateral and ventral); 6 and 8, *californica* Banks, genital plate (lateral and ventral).

plate is lobed ventrally and apically recurved, giving a distinct barbed-hook appearance. That the caudal aspect of the genital plate in *S. hamata* (Fig. 7) is identical in shape with the dorsal aspect of the genital plate in *S. californica* (Fig. 8) suggests that these may be sister species.

Sialis cornuta Ross.—The terminal plate has the apical margins cleft, and each cleft lobe is produced into swollen bulbs that diverge laterally (Fig. 3). The genital plate is broad and convex and mesally bears a pair of straight, stocky arms (Fig. 3).

Sialis arvalis Ross.—The genital plate is hinged to the apical margins of the terminal plate and is attached ventrally to a clear, saclike membrane. The genital plate is strongly flanged basally and is apically produced into a pair of short fingers (Fig. 4). The terminal plate bears a pair of large lobes apically (not visible in Fig. 4).

Sialis joppa Ross.—The genital plate is broad but slightly constricted on the lateral margins. Apically, the genital plate is produced into a pair of short fingers (Fig. 15). Lateral to the genital plate and posterior to the terminal plates are a pair of clear, membranous extrusions.

Sialis iola Ross.—The genital plate is elongate, rectangular, and apically produced into a pair of short fingers. The terminal plate has the apex narrow and tapering to a blunt point (not visible in Fig. 16).

AEQUALIS GROUP

The Aequalis group consists of two western species (*nevadensis* Davis and *rotunda* Banks) and three eastern species (*aequalis* Banks, *contigua* Flint, and *vagans* Ross). This group is characterized by a large, relatively unspecialized genital plate devoid of setae and a large, flaplike sternum 9. Tergum 9 rarely bears a bulbous evagination.

Sialis rotunda Ross.—The genital plate is subdivided into two concave halves that serve as receptacles for the apical portion of the lateral plates (Fig. 9). Two stocky genital hooks arise from the median evaginated ridge on the genital plate. These hooks run parallel and are moderately recurved ventrad (Fig. 10). The terminal plate is quadrate and only slightly cleft (Fig. 9). The lateral plates are produced into a pair of blunt arms covered with dense setae on the dorsal margins (Fig. 9).

Sialis nevadensis Davis.—This species bears a very large, subrectangular genital plate that is slightly convex. The genital plate bears a small pair of short fingerlike projections on its upper surface (Fig. 13). Beneath each finger is a membranous region which appears white under light microscopy.

Sialis vagans Ross.—The genital plate is large and subrectangular from a lateral aspect (Fig. 11). Extruded mesally is a single arm that becomes strongly bulbous apically (Fig. 12). Two small, pointed fingers are produced on the apical portion of this bulb.

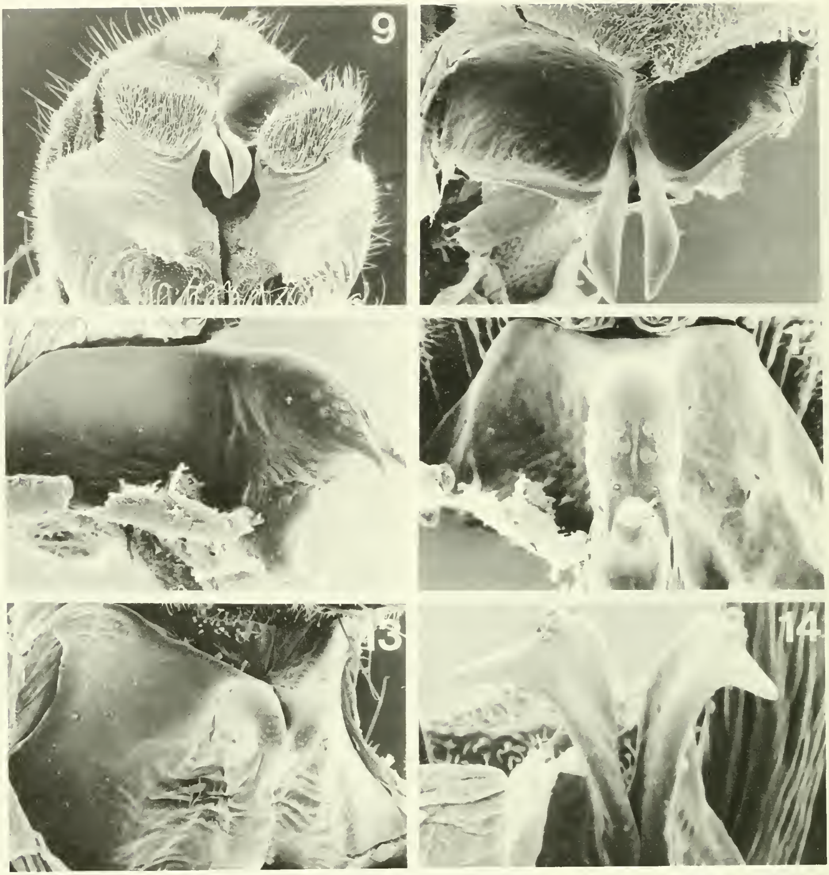
Sialis contigua Flint.—Basally, the genital plate is similar in size and shape to *S. vagans*. However, the median arm is narrower and the apical fingers are longer and diverge laterally from the medial point of attachment (Fig. 14). The terminal plate is U-shaped with the arms of the U closely appressed.

INFUMATA GROUP

The Infumata species group comprises eight species: *concava* Banks, *hasta* Ross, *infumata* Newman, *itasca* Ross, *mohri* Ross, *nina* Townsend, *spangleri* Flint, and *velata* Ross. All of these species are eastern or midwestern except *velata*, which occurs throughout North America. This group is characterized by a shield-shaped genital plate bearing a long pair of whiplike arms. The genital plate is completely fused to the basal portion of the terminal plate and is devoid of setae. The lateral plates are elongate, sternum 9 is moderately large, and tergum 9 lacks a bulbous evagination.

Sialis velata Ross.—The genital arms are long and curve 90 degrees before attaching to the genital plate. These arms fuse together before reaching the genital plate (Fig. 17) and bear a median lobe that is nearly one-half the length of the arms. The terminal plate, quadrate and slightly cleft, is basally fused to the genital plate.

Sialis mohri Ross.—The genital arms are long but stockier than *S. velata*. The median lobe of the genital arms is absent (Fig. 18). The terminal plate bears a pair of long, heavily sclerotized arms that converge medially (not visible in Fig. 18).



Figs. 9–14. Male genitalia of *Sialis* spp.: 9, *rotunda* Banks, lateral, genital, and terminal plates (ventral); 10, *rotunda* Banks, genital plate (ventral); 11 and 12, *vagans* Ross, genital plate (lateral and ventral); 13, *nevadensis* Davis, genital plate (lateral oblique); 14, *contigua* Flint, genital plate (ventral).

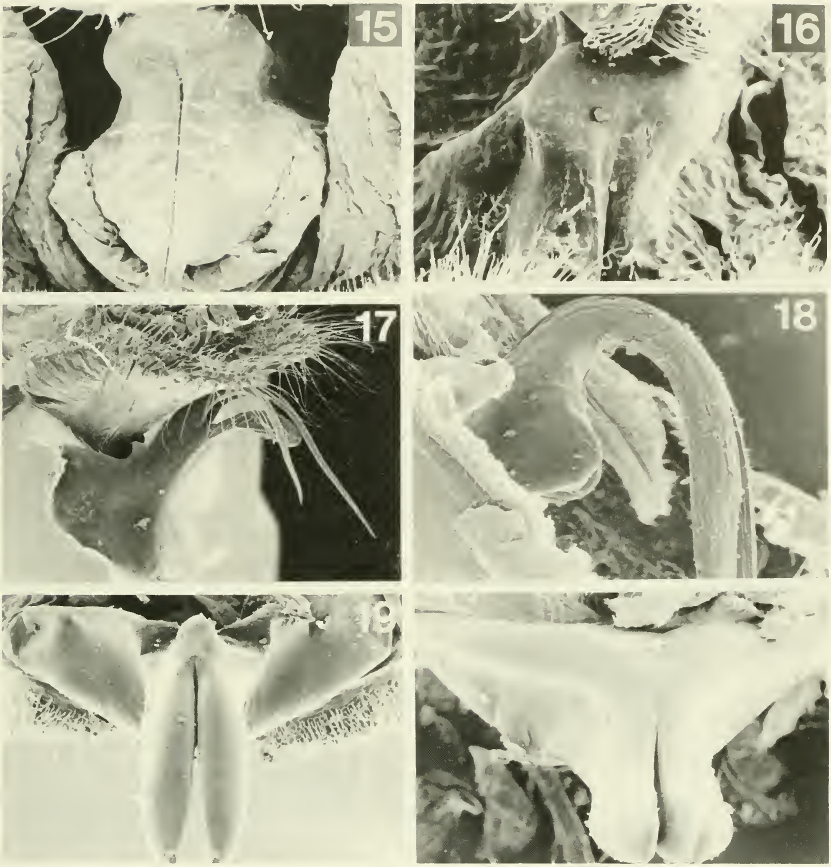
AMERICANA GROUP

The Americana species group consists of two eastern species: *americana* (Rambur) and *glabella* Ross. This group is distinguished by the large, unspecialized genital plate, moderately large sternum 9, and the unique, light red coloration of the body. The genital plate lacks setae, and sternum 9 lacks a bulbous evagination.

Sialis americana Rambur.—The genital plate is triangular and mesally bears a pair of long, broad arms (Figs. 19, 20). These arms run nearly parallel but diverge slightly laterally. The genital plate and arms do not bear setae.

DISCUSSION

The higher magnification and greater depth of field available make SEM a valuable tool for investigating evolutionary and taxonomic relationships within the *Sialis*. SEM analysis of North American *Sialis* has revealed that the genital structures are clearly diagnostic for all



Figs. 15–20. Male genitalia of *Sialis* spp.: 15, *joppa* Ross, genital plate (ventral); 16, *iola* Ross, upper half of genital plate (ventral); 17, *velata* Ross, genital and terminal plate (lateral oblique); 18, *mohri* Ross (lateral); 19 and 20, *americana* (Rambur) genital plate (ventral and dorsal).

14 species studied and that these structures are the key to understanding evolutionary relationships within the Sialidae.

All species identifications of adult Sialidae in North America have relied upon the key published by Ross (1937). After working with this key for several years, I have found that some couplets are ambiguous because they rely on characters that are either obscure or artificial. Compounding this problem are sketchy drawings that only partially reflect the actual structure. SEM analysis and light microscopy have revealed that there are characteristics better suited for species identification than those used in the key of Ross. Some of these characters are illustrated and outlined above. Therefore, use of these micrographs in conjunction with Ross's key will aid in more accurate identification of *Sialis* species.

ACKNOWLEDGMENTS

I thank Wilford M. Hess, James V. Allen, and Connie Swenson of the Electron Optics

Laboratory at Brigham Young University for their help with technical and critical aspects of scanning electron microscopy. I also thank Richard W. Baumann and Stephen L. Wood for reviewing early drafts of this manuscript.

LITERATURE CITED

CANTERBURY, L. E. 1978. Studies on the genus *Sialis* (Sialidae: Megaloptera) in eastern North America. Unpublished thesis, University of Louisville, Louisville, Kentucky. 93 pp.

EVANS, E. D. 1971. A study of the Megaloptera of the Pacific coastal region of the United States. Unpublished dissertation, Oregon State University, Corvallis. 210 pp.

FLINT, O. S. 1964. New species and new state records of *Sialis* (Neuroptera: Sialidae). Entomological News 75: 9–13.

ROSS, H. H. 1937. Studies of the Nearctic aquatic insects. I. Nearctic alderflies of the genus *Sialis* (Megaloptera: Sialidae). Bulletin of the Illinois Natural History Survey 21: 57–78.

TOWNSEND, L. H. 1939. A new species of *Sialis* (Megaloptera: Sialidae) from Kentucky. Proceedings of the Entomological Society of Washington 41: 224-226.

WHITING, M. F. 1991. A new species of *Sialis* (Megaloptera: Sialidae) from southern California. Great Basin Naturalist 51: 411–413.

Received 14 July 1990
Accepted 1 August 1991

Great Basin Naturalist 51(4), 1991, pp. 411–413

NEW SPECIES OF *SIALIS* FROM SOUTHERN CALIFORNIA (MEGALOPTERA: SIALIDAE)

Michael F. Whiting[1]

ABSTRACT.—*Sialis bilobata* is described as a new species of the alderfly family Sialidae from Los Angeles County, California. A brief description of the species, illustrations, and diagnosis that compares it with *Sialis arvalis* Ross are provided.

Key words: Sialis, *Sialidae, Megaloptera, Neuroptera, alderflies, aquatic insects.*

Alderflies are relatively rare semiaquatic insects found as adults along the margins of streams and lakes. Currently all alderflies in North America are placed in the genus *Sialis.* There have been 23 species of *Sialis* described from North America (Ross 1937, Townsend 1939, Flint 1964). During a study of phylogenetic relationships of the North American alderflies, I found an undescribed species among material loaned from Southern California. This new species is very interesting because it helps unravel the phylogenetic history of the Californica species group in western North America.

DIAGNOSIS

Sialis bilobata is most closely related to *S. arvalis* Ross and has been identified as such by previous workers. The terminal plate of *S. bilobata* swells apically to produce two large bulbous lobes that diverge laterally, whereas in *S. arvalis,* the apical portion of the terminal plate is only slightly swollen, and the small bulbs do not diverge but are contiguous mesally. From a lateral aspect (Fig. 1), the apical portion of the terminal plate in *S. bilobata* is more than twice as wide as the basal portion where swelling begins; in *S. arvalis* it is only slightly wider than the basal region. The genital plate in the two species is similar in shape, but in *S. bilobata* it is twice as large as in *S. arvalis.* In *S. bilobata* the plate is 0.144–0.154 mm in length; in *S. arvalis* it is 0.060–0.077 mm in length.

Sialis bilobata is distributed along the southern Pacific Coast and is known only from Ventura and Los Angeles counties in California. *S. arvalis* is distributed along the Pacific Coast from Douglas Co., Oregon, south to Santa Barbara Co., California.

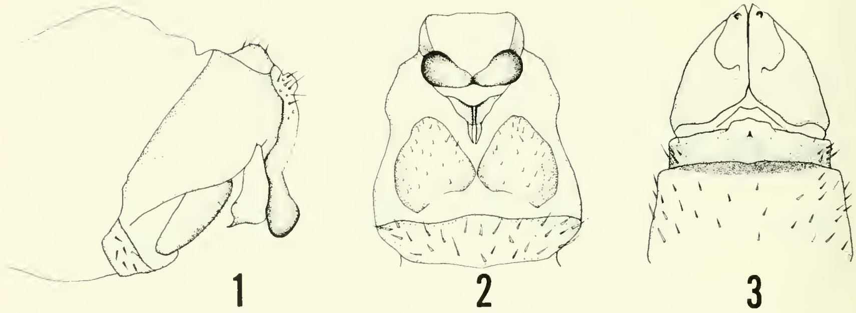
Sialis bilobata, n. sp.

MALE.—Body length 10.5–12.0 mm; wing length 9.2–10.0 mm. Head, body, and appendages black except: raised lines and dots on head and narrow ring around eye, yellowish; vertex clothed with abundant short setae; legs shading to brown; wings dark brown, slightly lighter towards apex. Sternum 9 narrow and bandlike, with sparse, short setae (Fig. 2). Lateral plates triangular, with middle portions closely appressed on meson. Genital plate small, quadrate, heavily sclerotized, and bearing short setae. Genital plate with a pair of short, closely appressed genital hooks attached basally which taper to a fine point. Genital plate basally attached to a clear, saclike membrane; membrane fused to ventral surface of terminal plate. Terminal plate U-shaped with apical margins swollen into two bulbous lobes diverging laterally (Fig. 2). From lateral aspect, these bulbs protrude caudally further than any other genital structure. Tergum 9 heavily sclerotized with a large extruded dorsal hump bearing coarse setae.

FEMALE.—Body length 12–14 mm; wing length 10.0–11.3 mm. Color and general structure as in male. Sternum 7 heavily sclerotized

---

[1] Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah 84602. Present address: Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853-0999.



Figs. 1–3. Genitalia of *Sialis bilobata* n.sp.: 1, ♂ (lateral); 2, ♂ (ventral); 3, ♀ (ventral).

and clothed with sparse setae (Fig. 3). Sternum 8 tilted, base depressed and apex raised; mesal portion slightly depressed longitudinally and bearing a heavily sclerotized spine; setae only moderately long mesally but longer laterally. Apical portion of segment bears a small, round depression on meson. Sternum 9 membranous but fairly rigid, forming a wide V.

TYPE MATERIAL.—The male holotype was collected from Brents Mountain Crags, Los Angeles Co., California, 20-V-1939, collector unknown; the female allotype is from Santa Ynez Canyon, Los Angeles Co., California, 30-III-57, V. A. Tucker. Paratypes are from the following localities: one male from Tapia Camp, Santa Monica Mountains, Los Angeles Co., California, 22-III-47, L. M. Martin; one male from Santa Ynez Canyon, Los Angeles Co., California, 30-III-57, V. A. Tucker; and one male from Ventura Co., Sespe Creek, 5 miles north of Fillmore, 1-IV-1981, R. W. Baumann & J. A. Stanger.

The holotype, allotype, and all paratypes except the Sespe Creek specimen are at the Los Angeles County Museum. The remaining paratype is in the Brigham Young University collection.

DISCUSSION

In Ross's taxonomic key to the Sialidae (1937), *S. bilobata* would come out in couplet 19b. with *S. arvalis*, but the two can be separated by the characters given above. According to the preliminary species groups as described by Ross (1937), *S. bilobata* is in the Californica species group. Based on phylogenetic analysis of morphological characters, *S. bilobata* appears to be very closely related to *S. arvalis*. Indeed, only these two species share the character of a uniquely shaped genital plate resting on a saclike membrane. That the distributions of both species are along the Pacific Coast further indicates that these species diverged from a common ancestor.

Evans (1971) designated an allotype for *S. arvalis* from a female collected from California, Ventura Co., Los Pardes National Forest, Sespe Creek, Sespe Gorge Campground, Hwy 33, 3-VI-1968, E. D. Evans. Because this specimen was collected from a locality in which *S. bilobata* is known, it is probable that this allotype is a female *S. bilobata*. Because the females of these species are identical in appearance, no known morphological data can be used to support or refute this supposition. Nevertheless, based on the distinct distributional range of the species, it is suggested that the allotype designation for *S. arvalis* be withdrawn.

ACKNOWLEDGMENTS

I thank Richard W. Baumann for helpful suggestions and Stephen L. Wood for reviewing early drafts of this manuscript. Thanks are also extended to Charlie Hogue at the Los Angeles County Museum for the loan of specimens and to Sun Yung Kim for making the illustrations.

REFERENCES CITED

EVANS, E. D. 1971. A study of the Megaloptera of the Pacific coastal region of the United States. Unpublished dissertation, Oregon State University, Corvallis. 210 pp.

FLINT, O. S. 1964. New species and new state records of *Sialis* (Neuroptera: Sialidae). Entomological News 75: 9–13.

ROSS, H. H. 1937. Studies of the Nearctic aquatic insects. I. Nearctic alderflies of the genus *Sialis* (Megaloptera: Sialidae). Bulletin of the Illinois Natural History Survey 21: 57–78.

TOWNSEND, L. H. 1939. A new species of *Sialis* (Megaloptera: Sialidae) from Kentucky. Proceedings of the Entomological Society of Washington 41: 224-226.

Received 20 June 1990
Accepted 1 August 1991

Great Basin Naturalist 51(4), 1991, pp. 414–415

UNUSUAL FORM OF *OPUNTIA RAMOSISSIMA* ENGELMANN

Allan R. Taylor[1]

Key words: Opuntia ramosissima; *diamond cholla; Clark County, Nevada; Spring Mountains, Nevada; Lee Canyon, Nevada; Kyle Canyon, Nevada; dwarf cholla.*

An interesting and evidently unique population of *Opuntia ramosissima* Engelmann (diamond cholla) has recently been observed in the middle reaches of Lee Canyon, in the Spring Mountains of Clark County, Nevada. The population was first noted at its upper limit, at around 5000 feet. Subsequent investigation shows that the range of this particular population is entirely west of Highway 93, between 3800 and 5300 feet on both sides of State Highway 156.[2]

This form of *O. ramosissima* is decidedly dwarf, as might be expected of a low-altitude plant somehow translocated to an elevation higher than the norm for the taxon. (Benson 1982 indicates 3000 feet as the upper limit of *O. ramosissima.*) The plant is low, even a mat-former; to describe it as a cactaceous *krumholz* would not be amiss.

If the morphology and other traits of the plants in this interesting population should prove to be different enough to warrant varietal status, I would suggest that names denoting low, small, or dwarf would all be appropriate for the form.

The plants tend to be only one or two joints tall (Fig. 1), but with abundant, rather tightly packed branches. Younger plants usually have heavy yellow-brown spination, but the older plants, sinuous and very woody, are almost entirely naked. The color of the joints is typically amethyst purple, although collected plants growing in pots in the greenhouse are pale green.

Clumps were encountered in habitat undoubtedly many years old; numerous dead clumps were also noted, invariably very old plants. Plants, both living and dead, are sparse until around 5000 feet, when they become more abundant.

Reproduction appears to be sexual, but no very small seedlings were encountered. The clumps are almost always in the open; thus, it is not likely that the plant requires the aid of a nurse plant to germinate and become established.

Companion plants are those that are characteristic of the eastern Mojave Desert: *Yucca schidigera*, *Larrea tridentata*, *Echinocereus engelmannii*, *Echinocactus polycephalus*, and *Malva* ssp. at the lower limit of the plant's distribution, progressing upward through *Opuntia acanthocarpa*, *O. multigeniculata*, *Tetrademia* ssp., *Chrysothamnus* ssp., *Atriplex* ssp., and *Ephedra* sp., with *Coleogyne ramosissima* and *Yucca brevifolia* var. *jaegeriana* dominant at the upper limit. *Coryphantha vivipara* var. *rosea*, which is relatively abundant in the higher reaches of the canyon, barely overlaps with *O. ramosissima* at the latter's upper limit. Of note also is that *Opuntia basilaris* occurs throughout the range of *O. ramosissima*, from the lowest elevations to the highest at which the taxon occurs.

Because individuals from this population have not been grown as yet under controlled conditions, it is not known whether the dwarf habit of the plants is an environmentally induced or a genetic trait. (Preliminary indications are that the size and form of the plant are genetically determined.) Cuttings from the population survived −25 F under snow in Boulder, Colorado, during the unseasonal cold of February 1989; so it appears likely

---

[1] Department of Linguistics, Box 295, University of Colorado, Boulder, Colorado 80309-0295.

[2] These interesting plants are not abundant in the area investigated. For example, when one stands at the location of one plant, it is unusual to see more than three or four other plants in the surrounding area. On the other hand, it is not rare either—many plants were discovered in the fifty or so acres surveyed.

Collection should be avoided, and it is indeed not necessary. I have supplied propagation material to the Nut House Nursery at Littlefield, Arizona, where interested persons can purchase established cuttings.

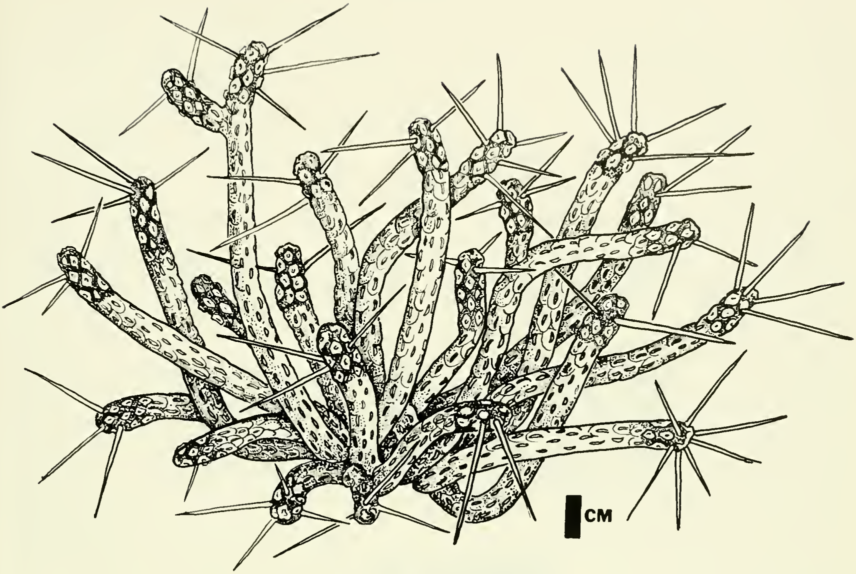


Fig. 1. *Opuntia ramosissima* Engelmann.

that the high-altitude form has greater frost tolerance than those from the more typically low-altitude habitats favored by this taxon.

Still to be determined is the complete range of this form: it would be surprising if it did not occur elsewhere in the vicinity. An obvious place to look is nearby Kyle Canyon, but appropriate elevations should be checked throughout the Spring Mountains and other ranges of southern Clark County.

ACKNOWLEDGMENTS

I thank Kaye Thorne, Brigham Young University Herbarium, for the illustration of *O. ramosissima* Engelmann.

LITERATURE CITED

BENSON, LYMAN. 1982. The cacti of the United States and Canada. Stanford University Press, Stanford, California.

Received 30 April 1990
Accepted 19 August 1991

THE
GREAT BASIN
NATURALIST

INDEX

VOLUME 51 — 1991

BRIGHAM YOUNG UNIVERSITY

Great Basin Naturalist 51(4), 1991, pp. 418–422

INDEX
Volume 51—1991

AUTHOR INDEX

Agenbroad, Larry D., 336
Anderson, Stanley H., 249
Apa, Anthony D., 301

Barber, Harry A., 343
Bauer, Karen Lyn, 226
Best, Louis B., 261
Blackwell, Boyde H., 343
Brotherson, Jack D., 153

Colwell, Robert K., 348

Davis, James N., 153
Deacon, James E., 256

Eddleman, Lee E., 236

Flinders, Jerran T., 205, 343
Frost, Grant T., 343

Gessaman, James A., 244
Grant, Gerold, 267
Guenther, Paula M., 282

Harper, Kimball T., 167, 397
Ho, Chih-Hsiang, 256
Hubert, Wayne A., 282
Hunter, Richard, 176

Inskeep, W. P., 271

Jensen, Richard D., 1
Johansen, Jeffrey R., 310
Johnson, D. A., 192

Kennedy, Thomas, 267
Koehler, David K., 249
Kuda, Derek, 267

Leininger, Wayne C., 286
Linder, Raymond L., 301
Lindzey, Frederick G., 244

Martin, Laurie, 267
Masters, Robert A., 316
McPherson, Guy R., 316
Mead, Jim I., 336
Medlyn, David A., 325
Moyle, Peter B., 267

Naeem, Shahid, 348
Nelson, Deanna R., 167, 397

OConnor, Barry M., 348

Pekins, Peter J., 244
Petersen, Kenneth L., 261
Prodgers, R. A., 271

Rasmussen, G. Allen, 316
Raynie, Douglas E., 397
Reid, Jody N., 1
Richardson, W. Scott, 293
Rogers, Mary Anne, 109, 127
Rumbaugh, M. D., 192

Schultz, Brad W., 183
Sharpe, Saxon E., 336
Shulz, Terri Tucker, 286
Smith, Nathan M., 1
Smith, Tom S., 205
Spence, John R., 279

Tausch, R. J., 183
Taylor, Allan R., 414
Tidwell, William D., 325
Tippie, Dallas, 256
Tueller, Paul T., 183

Uresk, Daniel W., 301

Vaitkus, Milda R., 236
Warrick, Robert B., 296
Welsh, Stanley L., 377
Wester, David B., 316
Whiting, Michael F., 404, 411
Williams, C. Frank, 296
Winn, David S., 205

KEY WORD INDEX

Among the key words listed below are the names of several taxa set in **boldface** type. These taxa are new to science.

Abies lasiocarpa, 244
alderflies, 404, 411
alkaloids, 397
aquatic insects, 411
Arctomecon, 397
    humilis, 167
Ascidae, 348
Aurealcaulis, 325
    bransonii, 331
    moorei, 326

behavior, 343
big sagebrush, 261
bighorn, 336
bighorn sheep, 205
birds, 286
bison, 336
Bison, 336
Blue Grouse, 244
bobcat, 343
break-away harness, 343
Bromus
    rubens, 176
    tectorum, 176

California
    Eagle Lake, 267
Capitol Reef National Park, Utah, 279
cattle grazing, 286
Cercocarpus, 153
checklist, 296
Clark County, Nevada, 414
Colorado, 286
Colorado Plateau, 336
competition, 256, 316
cryptogamic plants, 279
cultivated trees, 296
curlleaf mahogany, 183
Cynomys ludovicianus, 301

deer mice, 249
Dendragapus obscurus, 244
diamond cholla, 414
diatom
    brackish water, 310
    morphology, 310
dissolved oxygen, 282
Distichlis spicata, 271
Douglas-fir, 244
dwarf bear-claw poppy, 167
dwarf cholla, 414

Eagle Lake, [California], 267
ecology, 192
ecophysiology, 192
electrophoresis, 127
Eocene, 325
Eremophila alpestris, 301
evolutionary differentiation, 127
exotic species, 256

Felis rufus, 343
fire
    propagation, 176
    recovery, 176
fish, 267
flower mite, 348
food
    selection, 249
    supplementation, 226

Garfield County, [Utah], 279
genetic variation, 127
geographic information system, 205
geographic variation, 109, 127
Grand County, [Utah], 293
granivorous guild, 301
Great Salt Lake, Utah, 310
gypsophily, 167

habitat, 293
    characteristics, 167
    evaluation procedure, 205
    relationships, 153
    selection, 249
herbivory, 316, 397
Holocene, 336
hummingbird, 348

Idaho, 261
inland saltgrass, 271
intraspecific competition, 183
introduced species, 176

Juniperus
    occidentalis, 236
    pinchotii, 316

karyotype, 127
kitten, 343
Kyle Canyon, Nevada, 414

Lahontan redside, 267
LaSal Mountains, Utah, 293
Lee Canyon, Nevada, 414
legume, 192
life cycle, 226

management, 153
Megaloptera, 404, 411

metal-contaminated soils, 271
minimum viable population, 205
montane vole, 249
morphological variation, 109
mortality, 343
mortality factors, 226
mountain-mahogany, 153

names, 377
nest-site selection, 261
Neuroptera, 404, 411
Nevada
    Clark County, 414
    Kyle Canyon, 414
    Lee Canyon, 414
    Nevada Test Site, 176
    Spring Mountains, 414
New Mexico, 325
    San Jose Formation, 325
    San Juan Basin, 325
nitrogen fixation, 192
nodulation, 192
North America, 377

Opuntia ramosissima, 414
Ord's kangaroo rat, 249
Osmundaceae, 325
Ovis canadensis, 205
    canadensis, 336
Oxytropis, 377
    arctica var. ***murrayi***, 383
    campestris var. ***roaldii***, 386

Papaveraceae, 397
pattern recognition, 205
Phaeodactylum, 310
phytomass production, 236
plant records, 293
pocket gophers, 109, 127
population
    control, 256
    dynamics, 183
preadaptation, 271
Proctolaelaps, 348
    belemensis ***cyanocompsae***, 366
    certator, 370
    contentiosus, 373
    contumex, 369
    jurgatus, 354
    mermillion, 357
    rabulatus, 363
Pseudotsuga menziesii, 244

radio telemetry, 343
rainbow trout, 267
rangeland, 192
redberry juniper, 316
relic area, 316
reservoir, 282
Rhizobium lupini, 192
riparian wildlife, 286
Rocky Mountains, 286
roost sites, 244

Sage Thrasher, 261
San Jose Formation, [New Mexico], 325
San Juan Basin, [New Mexico], 325
San Juan County, [Utah], 293
SEM, 404
sexual dimorphism, 109
shrubsteppe, 261
Sialidae, 404, 411
Sialis, 404, 411
    bilobata, 411
size-age-density relationships, 183
small mammals, 249, 286
Soap Lake, Washington, 310
soil nutrients, 316
springfish, 256
Spring Mountains, Nevada, 414
strychnine, 301
subalpine fir, 244
synonyms, 377

Thomomys townsendii, 109, 127
tiger beetle, 226
Townsend's ground squirrel, 249
tree size, 236
Trinidad, 348
types, 377

understory, 236
Utah, 343
    Capitol Reef National Park, 279
    Garfield County, 279
    Grand County, 293
    Great Salt Lake, 310
    LaSal Mountains, 293
    San Juan County, 293
    Washington County, 296
    Wayne County, 279

vascular plants, 293
vegetation pattern, 316

Washington
    Soap Lake, 310
Washington County, Utah, 296
Wayne County, [Utah], 279
western jumping mouse, 286
western juniper, 236
Wilson's Warbler, 286
winter, 282
    habitat, 244
Wyoming, 282

zinc phosphide, 301

TABLE OF CONTENTS

Volume 51

No. 1—March 1991

The *Great Basin Naturalist* 50-Year Index, Volumes 1—50, 1939–1990. . . . . Jody N. Reid, Richard D. Jensen, and Nathan M. Smith 1–108

No. 2—June 1991

Articles

Evolutionary differentiation within the northern Great Basin pocket gopher, *Thomomys townsendii*. I. Morphological variation . . . . Mary Anne Rogers 109

Evolutionary differentiation within the northern Great Basin pocket gopher, *Thomomys townsendii*. II. Genetic variation and biogeographic considerations . . . . Mary Anne Rogers 127

Ecological relationships of curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) communities in Utah and implications for management . . . . . James N. Davis and Jack D. Brotherson 153

Site characteristics and habitat requirements of the endangered dwarf bear-claw poppy (*Arctomecon humilis* Coville, Papaveraceae) . . . . Deanna R. Nelson and Kimball T. Harper 167

Bromus invasions on the Nevada Test Site: present status of *B. rubens* and *B. tectorum* with notes on their relationship to disturbance and altitude . . . . Richard Hunter 176

Size, age, and density relationships in curlleaf mahogany (*Cercocarpus ledifolius*) populations in western and central Nevada: competitive implications . . . . Brad W. Schultz, R. J. Tausch, and Paul T. Tueller 183

Field acetylene reduction rates of *Lupinus argenteus* along an elevational gradient . . . . M. D. Rumbaugh and D. A. Johnson 192

Guidelines for manuscripts submitted to the *Great Basin Naturalist* 200

No. 3—September 1991

Articles

Habitat evaluation procedure for Rocky Mountain bighorn sheep in the Intermountain West . . . . Tom S. Smith, Jerran T. Flinders, and David S. Winn 205

Observations on the developmental biology of *Cicindela arenicola* Rumpp (Coleoptera: Cicindelidae) . . . . Karen Lyn Bauer 226

Tree size and understory phytomass production in a western juniper woodland . . . . Milda R. Vaitkus and Lee E. Eddleman 236

Physical characteristics of Blue Grouse winter use-trees and roost sites . . . . Peter J. Pekins, Frederick G. Lindzey, and James A. Gessaman 244

Habitat use and food selection of small mammals near a sagebrush/crested wheatgrass interface in southeastern Idaho . . . . David K. Koehler and Stanley H. Anderson 249

Effects of convict cichlids on growth and recruitment of White River springfish . . . . Dallas Tippie, James E. Deacon, and Chih-Hsiang Ho 256

Nest-site selection by Sage Thrashers in southeastern Idaho . . . . Kenneth L. Petersen and Louis B. Best 261

Fishes of Bly Tunnel, Lassen County, California . . . . Peter B. Moyle, Thomas Kennedy, Derek Kuda, Laurie Martin, and Gerold Grant 267

Heavy metal tolerance of inland saltgrass (*Distichlis spicata*) . . . . R. A. Prodgers and W. P. Inskeep 271

Notes

Notes on cryptogamic plants of Utah: range extensions and species new to the state from Capitol Reef National Park . . . . . John R. Spence 279

Factors influencing dissolved oxygen concentrations during winter in small Wyoming reservoirs . . . . . Paula M. Guenther and Wayne A. Hubert 282

Nongame wildlife communities in grazed and ungrazed montane riparian sites . . . . . Terri Tucker Shulz and Wayne C. Leininger 286

New records of vascular plants on the LaSal Mountains, Utah . . . . . W. Scott Richardson 293

Checklist of the cultivated trees of St. George, Washington County, Utah . . . . . Robert B. Warrick and C. Frank Williams 296

No. 4—December 1991

Articles

Impacts of black-tailed prairie dog rodenticides on nontarget passerines . . . . . Anthony D. Apa, Daniel W. Uresk, and Raymond L. Linder 301

Morphological variability and cell wall composition of *Phaeodactylum tricornutum* (Bacillariophyceae) . . . . . Jeffrey R. Johansen 310

Vegetation and soil zonation associated with *Juniperus pinchotii* Sudw. trees . . . . . Guy R. McPherson, G. Allen Rasmussen, David B. Wester, and Robert A. Masters 316

Two new species of *Aurealcaulis* (Osmundaceae) from northwestern New Mexico . . . . . William D. Tidwell and David A. Medlyn 325

Holocene bison from Arches National Park, southeastern Utah . . . . . Jim I. Mead, Saxon E. Sharpe, and Larry D. Agenbroad 336

Radio harness system for bobcat kittens . . . . . Boyde H. Blackwell, Grant T. Frost, Jerran T. Flinders, and Harry A. Barber 343

Flower mites of Trinidad II. The genus *Proctolaelaps* (Acari: Ascidae) . . . . . Barry M. OConnor, Robert K. Colwell, and Shahid Naeem 348

Oxytropis DC.—names, basionyms, types, and synonyms—Flora North America Project . . . . . Stanley L. Welsh 377

Alkaloidal relationships in the genus *Arctomecon* (Papaveraceae) and herbivory in *A. humilis* . . . . . Douglas E. Raynie, Deanna R. Nelson, and Kimball T. Harper 397

Scanning electron microscopic study of the male genitalia of the North American alderfly genus *Sialis* (Megaloptera: Sialidae) . . . . . Michael F. Whiting 404

New species of *Sialis* from Southern California (Megaloptera: Sialidae) . . . . . Michael F. Whiting 411

Note

Unusual form of *Opuntia ramosissima* Engelmann . . . . . Allan R. Taylor 414

Index to Volume 51 417

1 75 [illegible]

INFORMATION FOR AUTHORS

The *Great Basin Naturalist* welcomes previously unpublished manuscripts pertaining to the biological natural history of western North America. Preference will be given to concise manuscripts of up to 12,000 words.

SUBMIT MANUSCRIPTS to James R. Barnes, Editor, *Great Basin Naturalist*, 290 MLBM, Brigham Young University, Provo, Utah 84602. A cover letter accompanying the manuscript must include phone number(s) of the author submitting the manuscript; it must also provide information describing the extent to which data, text, or illustrations have been used in other papers or books that are published, in press, submitted, or soon to be submitted elsewhere. Authors should adhere to the following guidelines; manuscripts not so prepared may be returned for revision.

MANUSCRIPT PREPARATION. Consult Vol. 51, No. 2 of this journal for specific instructions on style and format. These instructions, GUIDELINES FOR MANUSCRIPTS SUBMITTED TO THE GREAT BASIN NATURALIST, supply greater detail than those presented here in condensed form. The guidelines are printed at the back of the issue; additional copies are available from the editor upon request. Also, check the most recent issue of the *Great Basin Naturalist* for changes and refer to the *CBE Style Manual*, 5th edition (Council of Biology Editors, One Illinois Center, Suite 200, 111 East Wacker Drive, Chicago, IL 60601-4298 USA, PHONE: (312) 616-0800, FAX: (312) 616-0226; $24).

TYPE AND DOUBLE SPACE all materials, including literature cited, table headings, and figure legends. Avoid hyphenated words at right-hand margins. Underline words to be printed in italics. Use standard bond (22 × 28 cm), leaving 2.5-cm margins on all sides.

SUBMIT 3 COPIES of the manuscript and the original on a 5.25- or 3.5-inch disk utilizing WordPerfect 4.2 or above. Number all pages and assemble each copy separately: title page, abstract and key words, text, acknowledgments, literature cited, appendices, tables, figure legends, figures.

TITLE PAGE includes an informative title no longer than 15 words, names and addresses of authors, a running head of fewer than 40 letters and spaces, footnotes to indicate change of address and author to whom correspondence should be addressed if other than the first author.

ABSTRACT states the purpose, methods, results, and conclusions of the research. It is followed by 6–12 key words, listed in order of decreasing importance, to be used for indexing.

TEXT has centered main headings printed in all capital letters; second-level headings are centered in upper- and lowercase letters; third-level headings begin paragraphs.

VOUCHER SPECIMENS. Authors are encouraged to designate, properly prepare, label, and deposit high-quality voucher specimens and cultures documenting their research in an established permanent collection, and to cite the repository in publication.

REFERENCES IN THE TEXT are cited by author and date: e.g., Martin (1989) or (Martin 1989). Multiple citations should be separated by commas and listed in chronological order. Use " et al." after name of first author for citations having more than two authors.

ACKNOWLEDGMENTS, under a centered main heading, include special publication numbers when appropriate.

LITERATURE CITED, also under a centered main heading, lists references alphabetically in the following formats:

Mack, G. D., and L. D. Flake. 1980. Habitat relationships of waterfowl broods on South Dakota stock ponds. Journal of Wildlife Management 44: 695–700.

Sousa, W. P. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101–124 *in* S. T. A. Pickett and P. S. White, eds., The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Coulson, R. N., and J. A. Witter. 1984, Forest entomology: ecology and management. John Wiley and Sons, Inc., New York. 669 pp.

TABLES are double spaced on separate sheets and designed to fit the width of either a single column or a page. Use lowercase letters to indicate footnotes.

PHOTOCOPIES OF FIGURES are submitted initially with the manuscript; editors may suggest changes. Lettering on figures should be large enough to withstand reduction to one- or two-column width. Originals must be no larger than 22 × 28 cm.

NOTES. If your manuscript would be more appropriate as a short communication or note, follow the above instructions but do not include an abstract.

A CHARGE of $45 per page is made for articles published; the rate for subscribers will be $40 per page. However, manuscripts with complex tables and/or numerous half-tones will be assessed an additional charge. Reprints may be purchased at the time of publication (an order form is sent with the proofs).

FINAL CHECK:

- Cover letter explains any duplication of information and provides phone number(s)
- 3 copies of the manuscript and WordPerfect disk
- Conformity with instructions
- Photocopies of illustrations

(ISSN 0017-3614)

GREAT BASIN NATURALIST Vol. 51, No. 4, December 1991

CONTENTS

Articles

Impacts of black-tailed prairie dog rodenticides on nontarget passerines.......... Anthony D. Apa, Daniel W. Uresk, and Raymond L. Linder 301

Morphological variability and cell wall composition of *Phaeodactylum tricornutum* (Bacillariophyceae) .... Jeffrey R. Johansen 310

Vegetation and soil zonation associated with *Juniperus pinchotii* Sudw. trees .... Guy R. McPherson, G. Allen Rasmussen, David B. Wester, and Robert A. Masters 316

Two new species of *Aurealcaulis* (Osmundaceae) from northwestern New Mexico .... William D. Tidwell and David A. Medlyn 325

Holocene bison from Arches National Park, southeastern Utah .... Jim I. Mead, Saxon E. Sharpe, and Larry D. Agenbroad 336

Radio harness system for bobcat kittens.............. Boyde H. Blackwell, ... Grant T. Frost, Jerran T. Flinders, and Harry A. Barber 343

Flower mites of Trinidad II. The genus *Proctolaelaps* (Acari: Ascidae) ....Barry M. OConnor, Robert K. Colwell, and Shahid Naeem 348

Oxytropis DC.—names, basionyms, types, and synonyms—Flora North America Project..................................Stanley L. Welsh 377

Alkaloidal relationships in the genus *Arctomecon* (Papaveraceae) and herbivory in *A. humilis*.................. Douglas E. Raynie, Deanna R. Nelson, and Kimball T. Harper 397

Scanning electron microscopic study of the male genitalia of the North American alderfly genus *Sialis* (Megaloptera: Sialidae) .....Michael F. Whiting 404

New species of *Sialis* from Southern California (Megaloptera: Sialidae)...... ....Michael F. Whiting 411

Note

Unusual form of *Opuntia ramosissima* Engelmann...........Allan R. Taylor 414

Index to Volume 51 417

3 2044 072 231 178